The Macrosemiidae, a Mesozoic family of holostean fishes

A. W. H. Bartram
late of Department of Biology, Queen Elizabeth College, Campden Hill, London W8 7AH

Contents

Bull. Br. Mus. nat. Hist. (Geol.) **29** (2): 137–234 Issued 22 December 1977

Summary

The fishes placed in the holostean family Macrosemiidae by a succession of authors have been re-examined. The group has been found to be polyphyletic. With the removal of four of the genera (*Uarbryichthys*, *Ophiopsis*, *Songanella* and *Aphanepygus*) and one species (*Macrosemius maeseni*), the remainder form a monophyletic group based upon two unique specializations. The genus *Euchelyolepis* is too poorly known to be assigned to the macrosemiids with certainty but it is provisionally retained in that family here. *Uarbryichthys* is shown to have acquired one unique specialization in parallel with *Macrosemius*, and is placed in a new family Uarbryichthyidae, the sister-group of the Macrosemiidae. These two groups are halecostome neopterygians in the sense of Patterson (1973), but show no evidence of relationship with either of the two main halecostome groups, the Halecomorphi or the Teleostei. Neither can the Macrosemiidae be shown to belong to any other halecostome group, and thus the family is classified as Halecostomi, subdivision *incertae sedis*.

Legnonotus krambergeri sp. nov. is described.

Introduction

The holostean fish family Macrosemiidae was established long ago by Thiollière (1858). Woodward (1895) gave a formal description of the group and considered them related to the Caturidae, and no subsequent worker has seriously questioned this view. Saint-Seine (1949) published the most detailed account to date of some members of the family. However, the bones of the skull of these fishes are so delicate that adequate preparative techniques are needed for their structure to be properly interpreted. For this reason, acetic acid preparation has been used in this investigation.

The primary aim of the present study has been to establish the Macrosemiidae as a monophyletic group, if possible, on the basis of shared, unique specializations. The remaining specializations of the family have been compared with those of other actinopterygians, to place the macrosemiids within a cladistic scheme of relationships and to see whether Woodward was right in deriving them from the caturids.

Unfortunately, this study has been hampered by two factors. Firstly, specimens of macrosemiids are comparatively rare. Secondly, the number of specimens available for acetic acid preparation was limited. Consequently, it has been impossible to give a full account either of the anatomy of most of the species, or of the variation between individuals within a species. Nevertheless, it is hoped that enough new information has been obtained for the objectives outlined above to have been reached.

Acknowledgements and material

I owe my thanks to the following persons for their kindness in allowing me to borrow or examine material from the collections in their charge; the abbreviations given in square brackets are those used in the text to indicate specimens in the collection.

Dr C. Patterson, British Museum (Natural History), London [BM(NH)], who also kindly corrected and commented upon the typescript; Prof. F. Mayr, Naturwissenschaftlichen Sammlungen, Eichstätt/Bayern [Ei]; Dr K. Felser, Institut für Geologie und Lagerstättenlehre der Montanistischen Hochschule, Leoben [Leo]; Dr S. M. Andrews, Royal Scottish Museum, Edinburgh [RSM]; Dr R. Dehm, Bayerische Staatssammlung für Paläontologie und historische Geologie, München [Mü]; Dr L. David, Muséum d'Histoire Naturelle, Lyon [LM]; Dr R. Lund, Carnegie Museum, Pittsburgh [CM]; Dr S. Wenz, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris [L]; Dr A. Ritchie, The Australian Museum, Sydney [AM]; Dr S. Rietschel, Natur-Museum Senckenberg, Frankfurt-am-Main [SM]; Dr H. Prescher, Staatliches Museum für Mineralogie und Geologie zu Dresden [DM]; Dr F. Westphal, Institut und Museum für Geologie und Paläontologie, Tübingen [Tü]; Dr K. Fischer, Paläontologisches Museum die Humboldt-Universität zu Berlin; Dr G. Pinna, Museo Civico di Storia Naturale, Milano [MM]; Prof. A. M. Maccagno, Istituto di Paleontologia dell'Università di Napoli [NM]; Dr P. Lane, Sedgwick Museum, Cambridge [CB].

In addition I wish to thank Queen Elizabeth College in the University of London for a Demonstratorship which enabled me to carry out this investigation, and also Professor Garth Chapman in whose Biology Department I worked. I am grateful also to the Central Research Funds Committee of the University of London for enabling me to visit museums in France and Germany. I thank Dr Bobb Schaeffer for lending me the preliminary notes he had made on the macrosemiids and Miss Alison Longbottom for helping me with the radiographs. Above all I am indebted to Dr Brian Gardiner who provided encouragement and continual enthusiasm while supervising the work.

Geological occurrence

The Macrosemiidae are extinct. The latest known members of the family, *Notagogus pentlandi* and *Propterus scacchi*, occur in the Lower Cretaceous (Barremian–Albian) of Pietraroia, Benevento and Castellamare, Italy. *Notagogus parvus* is present in the Lower Cretaceous (Wealden) of Bernissart, Belgium, while *N. ferreri* and *Propterus vidali* are found in the Neocomian of Lerida, Spain. The earliest known macrosemiids belong to the genus *Legnonotus*, from the Upper Triassic; *L. krambergeri* occurs at Hallein (Austria) and *L. cothamensis* is present in the Rhaetic of Gloucestershire. All the other macrosemiid species have been recovered from Upper Jurassic deposits of Europe. A brief discussion of the ecological conditions obtaining at the time of their deposition is given in the Ecological Note, pp. 225–6.

Uarbryichthys, which has been removed from the macrosemiids and classified as the plesiomorph sister-group of this family, occurs in the freshwater Jurassic deposits of New South Wales.

Techniques

Most macrosemiids have been collected from the Lower Kimmeridgian Lithographic Limestones of Eichstätt and Cerin. These matrices disintegrate in dilute acetic acid, and in the present work about a dozen specimens from the former locality have been prepared by the transfer technique of Toombs & Rixon (1959). These specimens were then examined with the aid of reflected and transmitted light, and of radiography.

Once the structure of the fishes had become familiar by the use of this technique, mechanical preparation could be used to advantage in the examination of specimens from other localities.

Systematic descriptions

Infraclass **NEOPTERYGII** (*sensu* Patterson 1973)

Division **HALECOSTOMI** (*sensu* Patterson 1973)

Subdivision ***incertae sedis***

Family **MACROSEMIIDAE** Thiollière 1858

Diagnosis. Small to large, laterally-compressed halecostome fishes; infra- and supraorbital sensory canals anastomosing behind the eye; supratemporals excluded from the midline; supratemporal commissure borne on the parietals; frontals forming an open trough housing the supraorbital canal over the ethmoidal region; nasals trough-like; rostral reduced to a short tube; vomer paired and toothed; parasphenoid toothless, forming basipterygoid processes and a pedicel at the entrance to the posterior myodome; exoccipital surrounding vagus foramen; epioccipital lining lateral cranial canal; sclerotic unossified; antorbital forming a tube around the infraorbital canal; nine infraorbitals, of which the first seven are scroll-like and the last two tubular; dermosphenotic fixed to skull roof; supraorbitals none to several; suborbitals absent; hyomandibular inclined anteroventrally, with head in the form of a quadrant facing anterodorsally and outer face of shaft forming an elongated flange alongside the anterior edge of the preopercular; symplectic short, and remote from mandible; metapterygoid in form of a disc lacking a large anterodorsal segment; two palatines and ectopterygoid toothed; gape small, the jaw articulation lying below or anterior to the orbitosphenoid; premaxillae immobile, with slender nasal processes; supramaxillae absent; mandible short, and deep at the level of the coronoid process, ventral border deeply concave, sensory canal housed in trough formed by dentary and angular; articular and retroarticular ossifying from Meckel's cartilage; quadratojugal long, stout, sometimes fusing distally with the quadrate; preopercular bent sharply forward beneath the orbit, the sensory canal exposed by large fenestrae; opercular tall and narrow with a convex lower border in contact with the subopercular; interopercular small and remote from lower jaw; seven or eight branchiostegals, the last three or four acinaciform; gular absent; hypohyal single; distal ceratohyal deep posteriorly; six supraneurals above anterior vertebrae, neural spines paired in caudal region, intermuscular bones absent; serrated appendage (clavicle?) present in pectoral girdle; dorsal fin long, divided in some genera; caudal fin forked or rounded, eight rays emanating from below the axial lobe, no epaxial fin-rays, uppermost fin-ray continuing into a scale row of the axial lobe, ural neural arches not elongated; scales rhomboid or cycloid, not broader than deep in ventral region; main lateral line terminating at base of axial lobe of caudal fin.

Genus *MACROSEMIUS* Agassiz 1844

Diagnosis. Large, elongate macrosemiid fishes; skull roof free from ganoine; supratemporals greatly reduced; cephalic division of main lateral line and supratemporal commissure exposed by large fenestrae; vomers bearing a transverse row of stout pointed teeth and a pair of large blunt teeth; ventral parts of anterior three infraorbitals expanded and overlapping the maxilla; gape very small, the quadrate articulation lying in front of the orbit; premaxilla with a single row of about four stout teeth; dentigerous expansion of maxilla shallow, upper and lower borders approximately parallel, the upper border forming a deep notch; maxillary teeth few and small; mandible with a single row of stout pointed teeth on dentary, prearticular and single coronoid bearing stout mammiliform teeth; palate fully ossified, ectopterygoid bearing about six tall stout teeth, two dermopalatines bearing similar teeth; anterodorsal edge of metapterygoid forming an obtuse angle; tooth plates on gill-arches bearing few, stout teeth; leading edge of preopercular forming sharp angle; opercular and subopercular ornamented with small, discrete tubercles of ganoine; uppermost branchiostegal ray devoid of ganoine; abdominal vertebral centra forming thick cylinders; pectoral fin with about 16 rays and six proximal radials, leading ray reduced to an unpaired spine, no fringing fulcra; pelvic fin formed by six rays preceded by a few small splints, fringing fulcra absent; anal fin profile convex, base extended, supported by six jointed, branching rays and an unjointed leading ray preceded by small splints, no fringing fulcra; caudal fin rounded, lower border armed with massive, median basal fulcra followed by fringing fulcra, small denticles on all rays except uppermost two or three, between three and five rays inserting onto the axial lobe, fringing fulcra on the uppermost fin-ray; dorsal fin single, extending from the occiput to the base of caudal fin, with between 32 and 39 rays each bearing denticles, leading ray preceded by two basal fulcra, fringing fulcra absent; region immediately on either side of dorsal fin devoid of scales; scales rhomboid, secondary transverse rows intervening between primary rows above the lateral line, scales below lateral line forming a pattern of rectangles.

Type species. *Macrosemius rostratus* Agassiz 1844.

INTRODUCTION. The genus *Macrosemius* was erected by Agassiz (1844) to contain a single species, *M. rostratus*, from the Lower Kimmeridgian of Bavaria. Thiollière (1873) recorded this species at the same horizon at Cerin (Ain, France), together with a new species, *M. helenae*. Sauvage (1883) described a very small form, *M. pectoralis*, from the Portlandian of Meuse, France. Woodward (1895) added two further species to the genus; these had previously been named *Disticholepis dumortieri* and *D. fourneti* by Thiollière (1873). Woodward also added *M. andrewsi* from the English Purbeck, and Eastman (1914a) described *M. dorsalis* from Bavaria. Woodward (1918) later transferred both *M. pectoralis* and *M. andrewsi* to a new genus, *Enchelyolepis*. Saint-Seine (1949) returned *M. dumortieri* and *M. fourneti* to Thiollière's genus *Disticholepis*. Later, Saint-Seine (*in* Saint-Seine & Casier 1962) described *M. maeseni* from the Upper Jurassic of Zaïre.

REMARKS. *Disticholepis* is very similar to *Macrosemius* and, following Woodward, is synonymized with that genus here. Eastman's *M. dorsalis*, founded upon a single specimen, probably belongs to *M. rostratus*, although, as he points out, the dorsal fin is taller than is usual for *rostratus*. *M. helenae* is synonymous with *Notagogus margaritae*, and *M. maeseni* is placed in the chondrostean genus *Tanaocrossus* Schaeffer (p. 207).

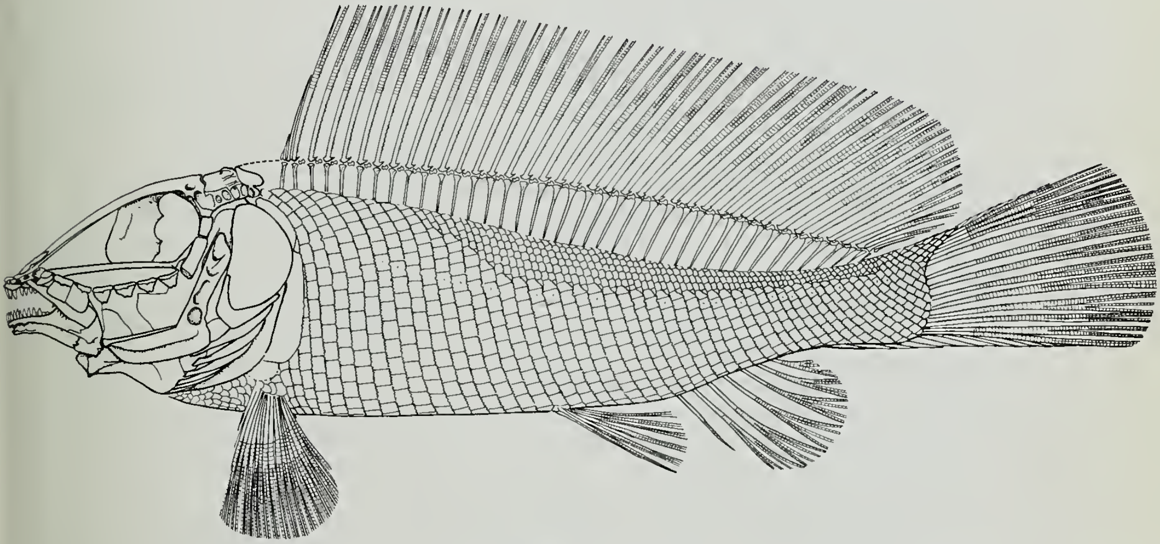

Fig. 1 *Macrosemius rostratus* Agassiz. Restoration of skeleton. × ½ approx.

Macrosemius rostratus Agassiz 1844

Figs 1–18; Pls 1–2

1836 *Macrosemius* Agassiz **2** : pl. D, fig. 3.
1844 *Macrosemius rostratus* Agassiz **2**, 2 : 150; pl. 47a, fig. 1.
1851 *Macrosemius latiusculus* Wagner : 74.
1851 *Macrosemius rostratus* Agassiz; Wagner : 73.
1863 *Macrosemius rostratus* Agassiz; Wagner : 647.
1863 *Macrosemius insignis* Wagner : 648; pl. 2.
1887 *Macrosemius latiusculus* Wagner; Zittel : 218, text-fig. 232.
1895 *Macrosemius latiusculus* Wagner; Woodward : 163, text-fig. 29.
1895 *Macrosemius rostratus* Agassiz; Woodward : 177; pl. 3, fig. 4.
1914a *Macrosemius rostratus* Agassiz; Eastman : 406; pl. 63, fig. 2.
1914a *Macrosemius dorsalis* Eastman : 406; pl. 65, fig. 2.
1966 *Macrosemius rostratus* Agassiz; Schultze : 275, text-figs 16b, 30.

DIAGNOSIS. *Macrosemius* with between 32 and 39 dorsal fin-rays; large basal fulcra along ventral border of caudal peduncle possessing straight edges; supraorbitals absent.

HOLOTYPE. Národnì Muzeum, Prague, T858, from the Eichstätt region of Bavaria.

HORIZON AND LOCALITIES. Lower Kimmeridgian of the Eichstätt and Kelheim regions of Bavaria.

MATERIAL. BM(NH): 37094, 37051, P7177, P956, P955, P3616; RSM: 1901.67.1; CM: 4453, 4765; Ei: 2 specimens; Mü: AS.1.769, AS.1.770, AS.1.640, AS.1.639, AS.6.24, 1954.1.530, 1904.1.18.

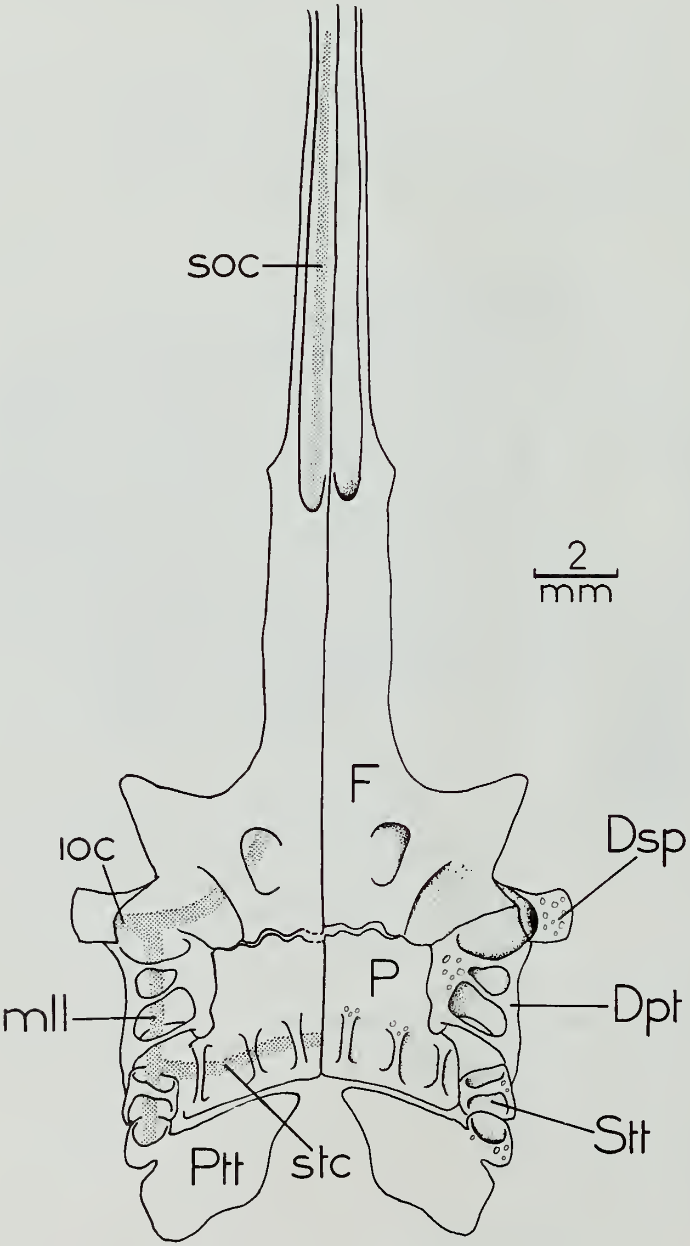

Fig. 2 *Macrosemius rostratus* Agassiz. Restoration of the skull roof of an immature individual, 37094.

DESCRIPTION. (i) General features. *M. rostratus* is a large, elongate fish reaching a standard length of about 220 mm. The trunk is shallow and tapers gradually to form a relatively deep caudal peduncle (Fig. 1).

(ii) Skull roof and braincase. As in the other members of the family, the postorbital region of the skull is short and compact. The form and relationship of the skull roof bones are displayed in 37094 (Fig. 2), although this individual is young (standard length 105 mm) and the bones may not have attained the adult pattern.

The frontals are constricted above the orbits and drawn out along the ethmoidal region. The parietals form a sinuous, non-overlapping suture with the frontals. The supratemporal commissure crossed the posterior part of the parietal; a delicate arch of bone, which spanned the canal, is preserved close to the midline, and the remains of another, lateral, arch may also be seen (Fig. 5). In older individuals these arches probably thickened only slightly, leaving the wide sensory canal exposed by large fenestrae; these are visible in specimens of *M. fourneti*, in which three such arches occur. The bases of the arches are perforated by small pores.

The supratemporal is a small, paired bone, excluded from the midline, forming a short tube around the cephalic section of the lateral line between the post-temporal and dermopterotic; the outer wall of the tube is reduced to a narrow strut. The supratemporal did not enclose the lateral part of the supratemporal commissure; the latter presumably joined the lateral line between the supratemporal and the dermopterotic. As is well known, the supratemporals of neopterygians arise in ontogeny as a transverse row of separate ossifications; in *Amia* and most extant teleosts, these fuse together to form paired supratemporals in the adult. In a few genera, however, the ossifications remain separate, as in *Lepisosteus*, *Sinamia* and *Dapedium*, for example. Jarvik (1967 : 191; fig. 5) has noted that in certain cypriniform teleosts the supratemporals fuse with the parietals, and that in rare individuals of *Polypterus* and *Acipenser* (1967 : fig. 6) fusion occurs between the medial supratemporal and the parietal. McDowell (1973 : 12) has since noted that in many other groups of teleosts (Notopteridae, Osteoglossoidei, Characidae, Gymnotidae) the supratemporal commissure is carried by paired bones which have hitherto been called parietals. The possibility exists, then, that a similar fusion has occurred in macrosemiids, and that the supratemporal commissure is borne by a compound parieto-supratemporal, rather than by a parietal which has come to occupy the hindmost part of the skull.

The dermopterotic extends along the lateral edge of the parietal and forms a suture with the frontal anteriorly. The cephalic portion of the lateral line occupied most of the width of the bone and was exposed by two large fenestrae bounded by three struts of bone. The sensory canal presumably joined the supraorbital canal in the space above the suture between the frontal and the dermopterotic, before turning downwards into the dermosphenotic as the infraorbital canal.

The lateral margin of the frontal forms a narrow tapering process over the posterior part of the orbit. The orbital embayment is very deep in this specimen; it was probably less marked in older individuals. Viewed from above, the frontal narrows further anteriorly, becoming very slender in the preorbital region. The supraorbital sensory canal passed into the frontal above the posterior limit of the orbit. The canal was exposed dorsally by a large fenestration as it passed through the bone toward the midline; the orbital wall of the canal is perforated by fine pores in this region (Fig. 5). The frontal forms a wide trough in the preorbital region, along which lay the supraorbital canal.

The right nasal is preserved in 37094 in a damaged condition (Fig. 8b). It formed a scroll around the anterior part of the supraorbital canal over the nasal process of the premaxilla. The rostral is not preserved in any of the specimens.

The vomer is paired and extends beneath the parasphenoid from the level of the orbitosphenoid, widening to form a broad contact with the dentigerous part of the premaxilla (Fig. 8b). The dorsal surface of the vomer in this region is shaped to receive the medial process of the maxilla. The vomerine teeth are visible in AS.1.770. A row of four stout, closely-set teeth occurs immediately posterior to, and parallel with, the premaxillary tooth-row. Each vomer bears in addition a large, laterally-compressed crushing tooth close to the midline behind the transverse row.

The left half of the braincase is incompletely preserved in medial view in specimen AS.1.640 (Fig. 3). The parasphenoid extends anteriorly from the basioccipital condyle and tapers to form

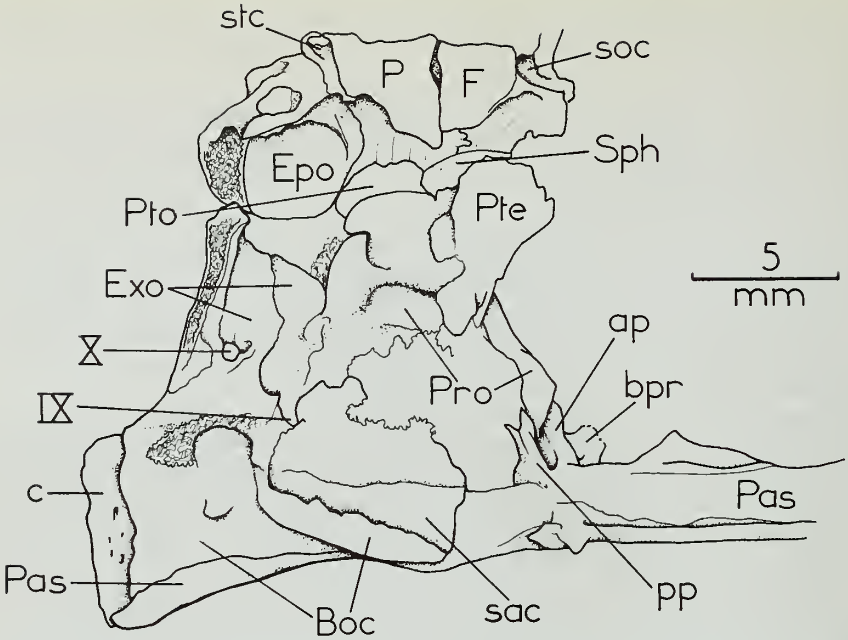

Fig. 3 *Macrosemius rostratus* Agassiz. Interior of the postorbital region of the braincase, as preserved in AS.1.769.

two prongs beneath the nasal processes of the premaxillae (Fig. 8a). The lateral edges of the parasphenoid below the orbit are marked by a deep longitudinal incision. Immediately posterior to this incision project a pair of stout basipterygoid processes, each with a shallow groove along the dorsal surface. The efferent pseudobranchial artery passed through a small canal ventral to the base of the process.

The basipterygoid process is united by a web of bone to the ascending process of the parasphenoid, which is inclined dorsolaterally and slightly posteriorly, supported by a thin buttress of bone (Fig. 5).

A short, stout pedicel, weakly forked at the tip, arises from the parasphenoid between the basipterygoid processes; this pedicel divides the entry of the posterior myodome into two. A small process has been reported in a similar position on the parasphenoids of the palaeoniscid *Kansasia eatoni* (Poplin 1974 : fig. 8) and of pholidophorid and leptolepid teleosts (Patterson 1975 : 517–27; figs 142–3).

The basioccipital is a massive bone beneath the foramen magnum whose floor, as usual, it forms. The first vertebral centrum appears to have been firmly fixed to the basioccipital condyle. Beneath the otic region the basioccipital forms the ventral part of a large, inflated, thin-walled chamber, supported along its ventral surface by a lateral expansion of the parasphenoid. This chamber housed the sacculus, which thus extended down to the level of the parasphenoid as it did, probably primitively, in *Australosomus* (Nielsen 1949 : fig. 9), *Pteronisculus* (Nielsen 1942 : fig. 14), *Lepisosteus* (Fig. 46) and *Amia*.

A posterior myodome almost certainly existed, the posterior rectus muscles passing into it on either side of the parasphenoid pedicel. Their origin was probably restricted to the deep recesses in the parasphenoid immediately posterior to the basipterygoid processes. Unfortunately the roof of the myodome, which would have formed from the prootics, is not preserved.

The glossopharyngeal nerve passed through a small foramen which pierces the posterior part of the wall of the saccular chamber in the basioccipital.

The exoccipital is partially fused at its base with the basioccipital and meets the posterior edge of the prootic; the vagus foramen is completely enclosed by the bone, as in *Lepisosteus* and

Lepidotes (Rayner 1948). A gap, cartilaginous in life, occurs between the dorsal edges of the exoccipital and prootic, and the epioccipital.

The epioccipital appears to be preserved in its natural position, with the exposed, medially-facing edge revealing cancellous endochondral bone. The internal wall of the epioccipital is approximately circular and forms a smooth surface; this indicates that, unlike the condition in *Amia*, the bone lined a cranial cavity. The epioccipital of *Lepisosteus* is similarly smooth (Rayner 1948: fig. 34) since it lines a large lateral cranial canal (Patterson 1975: fig. 111; Fig. 46). Rayner (1948 : 300) had sought for such a canal in larval *Lepisosteus* but reported its absence.

The lateral cranial canal of *Lepisosteus* occurs as usual in the wall of the braincase between the three semicircular canals. It is lined by cartilage except where this has been replaced by the epioccipital bone. It forms a connection with the median cranial cavity by means of a wide opening passing through the loop of the posterior semicircular canal, and of a much narrower tube passing through the loop of the anterior semicircular canal. The lateral cranial canal of *Lepisosteus* is filled with fatty tissue, as is the posterior part of the median cranial cavity; such tissue must increase the buoyancy of the fish. A lateral cranial canal has been recorded in *Caturus*, *Dapedium* (Rayner, 1948: figs 9, 15) and pholidophorids (Patterson 1975), but not in *Amia*. In teleosts, the medial wall of the lateral cranial canal fails to ossify in leptolepids (Patterson 1975: 413), and the canal is lost in living teleosts. But in living teleosts the inner face of the epioccipital is smooth (Allis, 1903: fig. 8; Goodrich 1930: fig. 599) and lines part of the cranial cavity. It is not known whether the smooth inner face of the epioccipital in *Macrosemius* lined a lateral cranial canal as in *Lepisosteus*, a primitive condition, or a part of the cranial cavity as in teleosts, a derived condition.

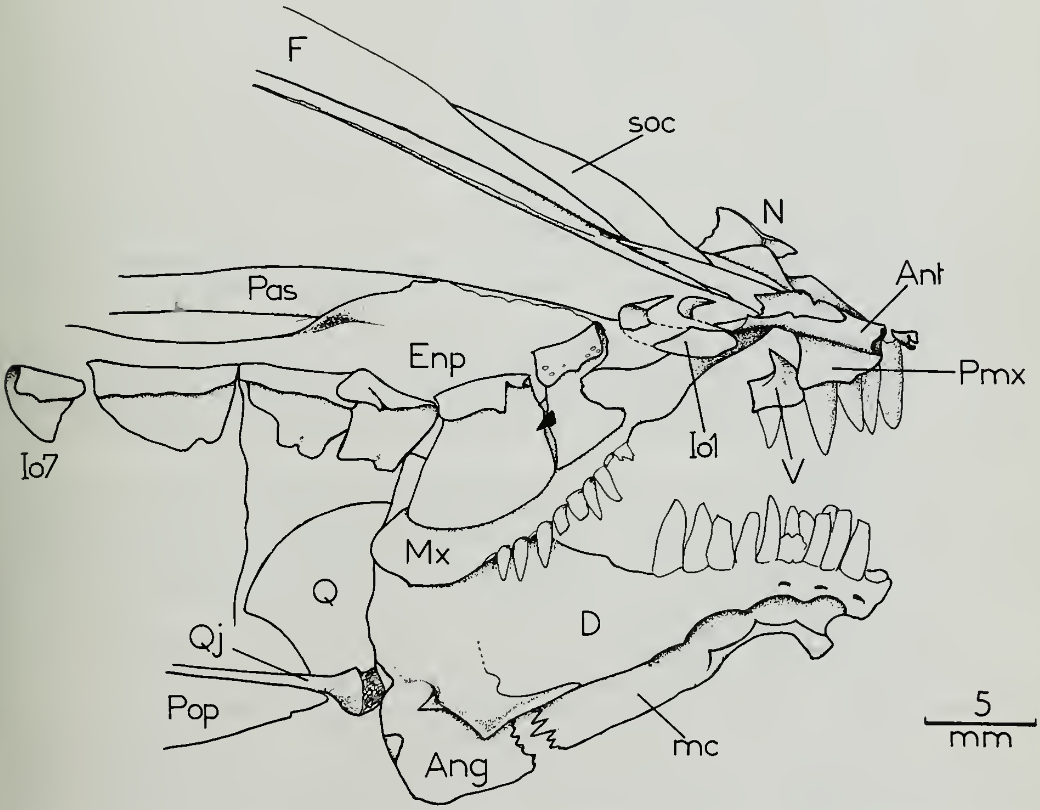

Fig. 4 *Macrosemius rostratus* Agassiz. Jaws and snout region in lateral view, as preserved in 37051.

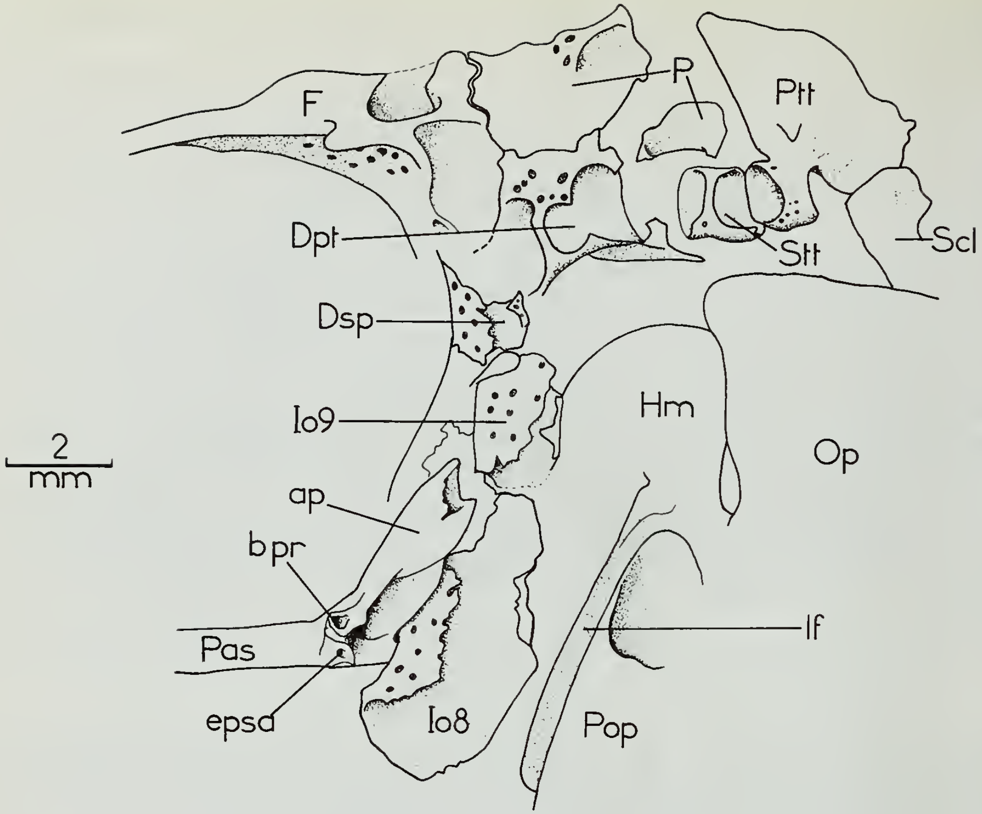

Fig. 5 *Macrosemius rostratus* Agassiz. Postorbital region of left side of skull, as preserved in 37094.

The epioccipital of *Macrosemius* also displays an unusual feature. The dorsal surface of the bone forms a shallow gutter whose relationship with the other cranial cavities is unclear; no such structure has been reported elsewhere. No supraoccipital is present in the specimen; this may be due to faulty preservation.

Patterson (1975 : 454) has suggested that the bone hitherto considered to be the epioccipital in *Lepisosteus* and *Lepidotes* may be the pterotic, the former having been lost. This is not the case in *Macrosemius*, however, where a small part of the pterotic is visible between the prootic and the skull roof. A small part of the sphenotic is also visible above the prootic, underlying the dermosphenotic.

The ventral half of the prootic, which formed the walls of the otolith chamber and the myodome, is not preserved. The posterior edge of the bone forms a stout flange which housed the ampulla of the horizontal semicircular canal, as in *Lepisosteus*. The inner surface of the prootic, immediately anterior to this flange, forms a recess presumably for the utriculus. Below this recess the bone becomes very thin; the region of the suture with the basioccipital is lost in the specimen. Part of the pterosphenoid, revealing its smooth medial surface, is also preserved.

The orbitosphenoid (Fig. 13) is preserved in AS.1.770. The bone lies unusually far forward between the frontal and the parasphenoid. The posterior edge forms several shallow embayments. Saint-Seine (1949 : fig. 88–89a) found a similar orbitosphenoid in *M. fourneti*.

Part of the preorbital region of the braincase is exposed in 37051. A long, stout ossification underlies the frontal and the nasal process of the premaxilla (Fig. 8b). It is not clear whether this dorsal ethmoid ossification is median or paired. No other ossifications of the snout region of the braincase are preserved.

(iii) Circumorbital bones. No supraorbitals are preserved in the available specimens of *M. rostratus*. Saint-Seine (1949 : 202) has reported their presence in *M. fourneti*. The infraorbital series comprises 11 bones: antorbital, nine infraorbitals and dermosphenotic. These are visible in 37051 and 37094.

The antorbital forms a long, gradually tapering tube around the anterior part of the infraorbital sensory canal. The canal was exposed by two large fenestrae which pierce the posterior part of the tube; two smaller openings occur in the narrow anterior part which curves medially across the premaxilla.

The first three infraorbitals (Fig. 4) cover the lateral surface of the maxilla when this is raised. They are thin sheets of bone whose upper margins curled over the dorsal surface of the infraorbital sensory canal. The following four infraorbitals lie below the orbit, and differ from the first three in lacking the ventral extension. The eighth and ninth infraorbitals lie behind the orbit (Fig. 5); both form complete tubes around the sensory canal, and the eighth is about twice the length of the ninth. The walls of the tubes are perforated by small holes.

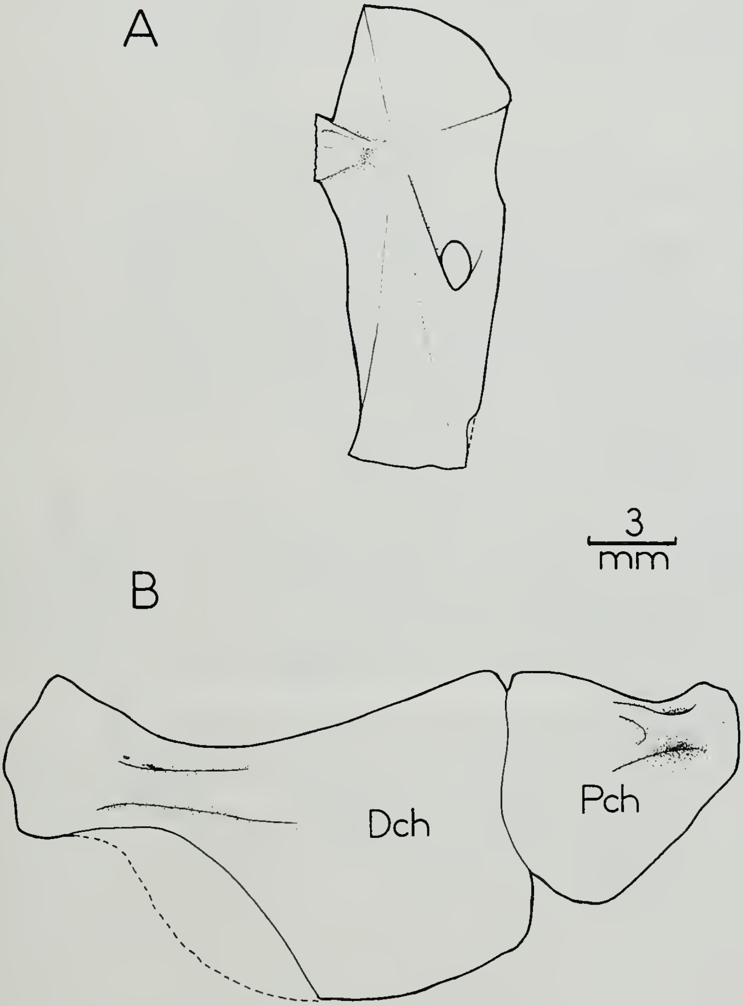

Fig. 6 *Macrosemius rostratus* Agassiz. A, isolated left hyomandibular in medial view. B, isolated right ceratohyal in medial view. AS.1.640.

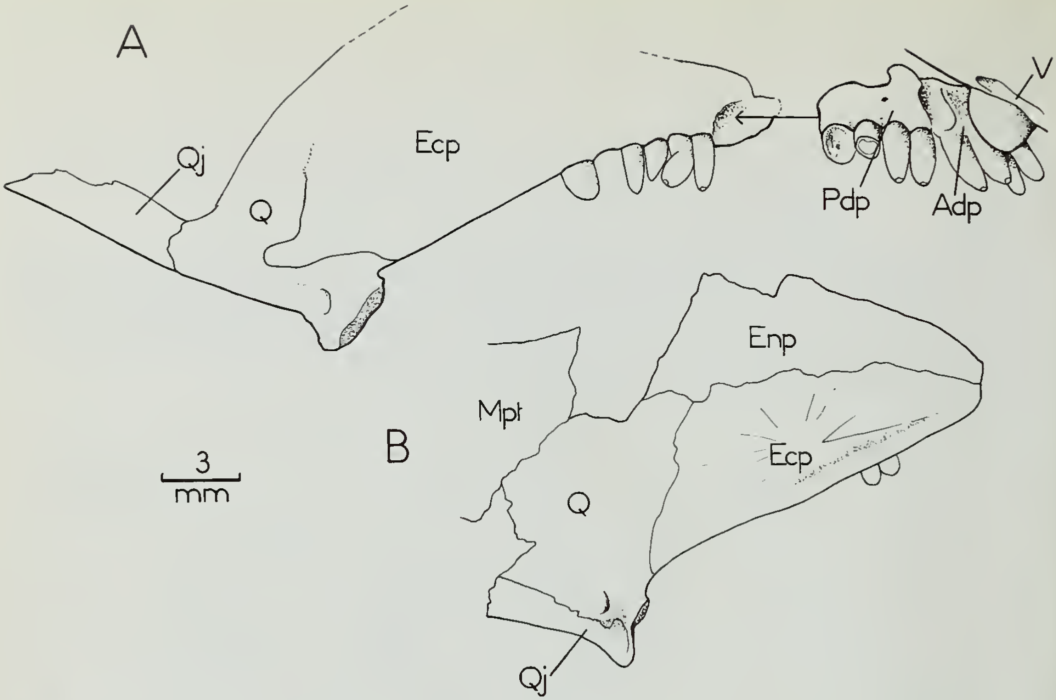

Fig. 7 *Macrosemius rostratus* Agassiz. Two views of the palate. A, medial view with palatines displaced forward, AS.1.770. B, lateral view, AS.1.640.

The dermosphenotic resembles the last two infraorbitals in forming a short, vertical, perforated tube around the sensory canal. The anterior wall of the tube extends along the orbital wall of the frontal, to which it was probably fixed. Thus, although not hinged to the skull roof as it is in *Lepisosteus*, the dermosphenotic of *Macrosemius* is not fully incorporated into the roof as in *Amia* but retains the characteristics of an infraorbital.

As in all other members of the Macrosemiidae, suborbitals are absent.

(iv) Hyopalatine bones. The hyomandibular is preserved in medial view in AS.1.640. The proximal articulatory facet forms a quadrant facing anterodorsally. The short, stout opercular process occurs about one-third of the way along the posterior edge from the proximal end (Fig. 6A). The foramen for the hyomandibular nerve pierces the bone close to the anterior edge, slightly below the mid-point along the length of the bone. The lateral surface of the hyomandibular (37051; Fig. 5) bears a narrow, anteriorly-inclined flange alongside the leading edge of the preopercular, forming an elongated recess.

The metapterygoid is not clearly exposed in any of the specimens. Its form approximates to that of a disc lacking a large anterodorsal segment; the two straight edges form an obtuse angle (Fig. 11). The upper, dorsally-inclined edge articulated with the basipterygoid process.

The remainder of the palate is preserved in medial view in AS.1.770, and in lateral view in AS.1.640 (Fig. 7). The quadrate is roughly triangular, with a convex posterodorsal edge which extends to the metapterygoid in older specimens. The articulatory facet on the quadrate is very broad and faces forward. The posteroventral edge of the quadrate is closely applied to an elongated bone of dermal origin which lies along the dorsal surface of the ventral arm of the preopercular. This elongated bone is covered by the quadrate along the anterior half of its medial surface. Its distal end is expanded and fits closely against the posterior surface of the thin lateral part of the quadrate condyle; fusion occurs between the two elements in this region. A bone of similar form and relationship with the preopercular and quadrate has been described by Patterson (1973 : fig. 26) in *Lepidotes* and *Dapedium* and identified by him as the quadratojugal.

The ectopterygoid has a complicated overlapping suture with the quadrate, which occupies only a very small length of the lateral border of the palate. The lateral border of the ectopterygoid bears a row of about six stout teeth, increasing in height anteriorly; the medial border forms a long straight suture with the endopterygoid. The endopterygoid bears no teeth.

Two dermopalatines precede the ectopterygoid; each bears four stout teeth, similar in size and form to those on the ectopterygoid.

(v) Dermal upper jaw. The premaxilla has a broad dentigerous head, produced dorsoposteriorly to form a slender nasal process. The premaxillary teeth form a transverse row of four or five; they are stout, laterally compressed and taper to a blunt point (Fig. 8). The slender, tapering nasal process sutures with the dorsal ethmoid ossification, beneath the nasal. The medial surface of the process is expanded to form a short, narrow gutter along which lay the olfactory nerve. A small foramen pierces the base of the nasal process close to the medial edge; this presumably transmitted the anterior palatine ramus of the facial nerve. A similar condition is found in *Amia* (Allis 1897 : pl. 21).

Anteriorly the maxilla forms a long, stout, cylindrical medial process which rotated in the space between the vomer and premaxilla (Fig. 8). The upper and lower edges of the maxillary expansion are approximately straight and parallel to each other; the posterior border is convex. The dorsal edge is incised by a deep, anteriorly-directed notch, about midway along its length. The oral border of the maxilla bears about eight sharply-pointed teeth, about half the size of those on the premaxilla (Fig. 4).

As in all other members of the family, the supramaxilla is absent.

(vi) Lower jaw. The short, anterior, dentigerous portion of the mandible is followed by a high coronoid process. The ventral border is markedly concave. Dentary, angular, surangular, prearticular, one coronoid, articular and retroarticular bones are present.

The lower jaw is exposed in medial view in AS.1.770 (Fig. 9). The articular facet is shallow, very broad, and faces posteriorly. Only the lower part of the broad coronoid process of the articular is preserved. A large retroarticular, formed partly of dermal bone, caps the posterior end of the angular, below the articular facet. The retroarticular does not form part of this facet.

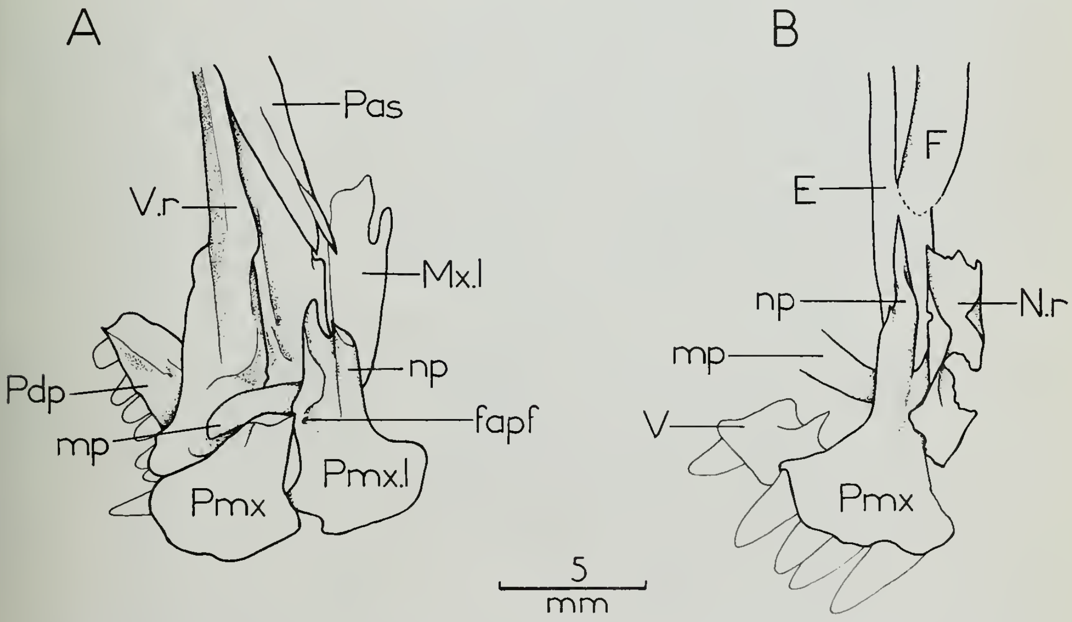

Fig. 8 *Macrosemius rostratus* Agassiz. Two dorsolateral views of the snout region. A, AS.1.640. B, 37051.

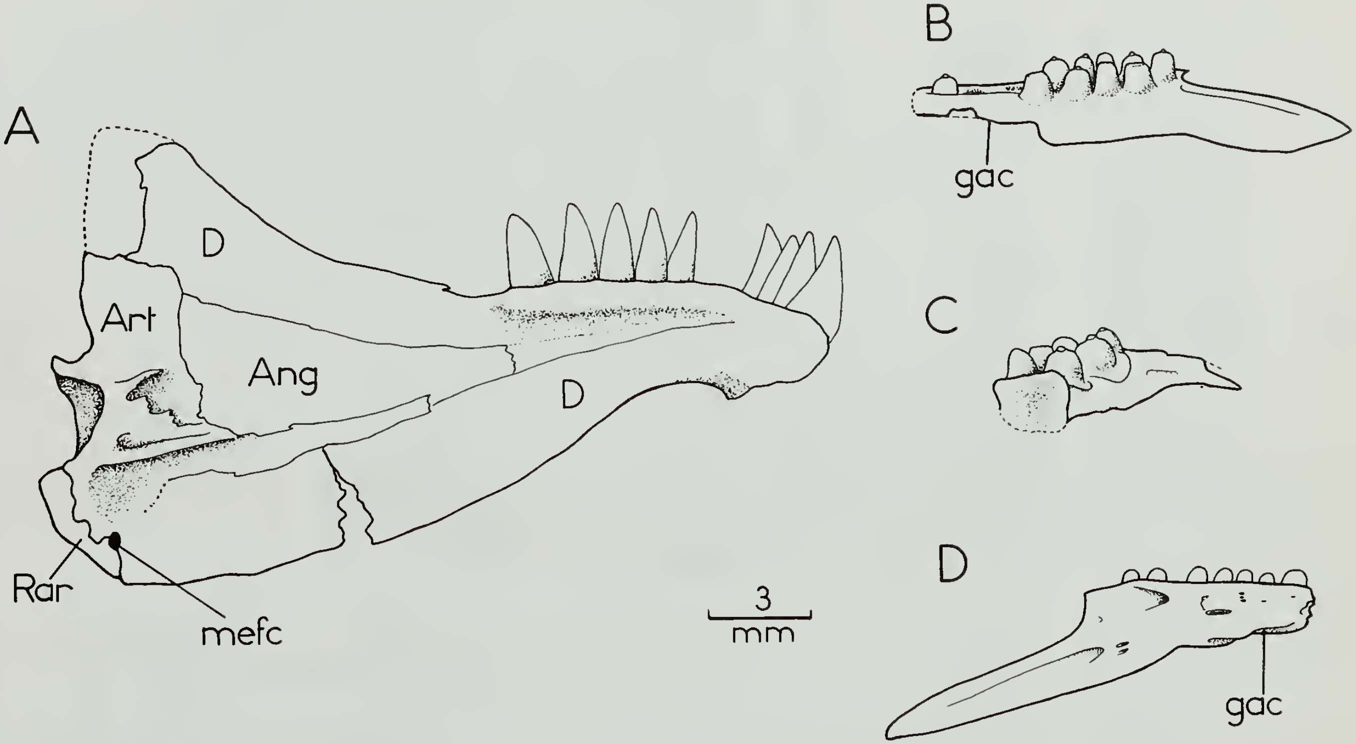

Fig. 9 *Macrosemius rostratus* Agassiz. Lower jaw. A, left mandible in medial view. B, right prearticular in medial view. C, right coronoid in medial view. All AS.1.770. D, right prearticular in lateral view, AS.1.639.

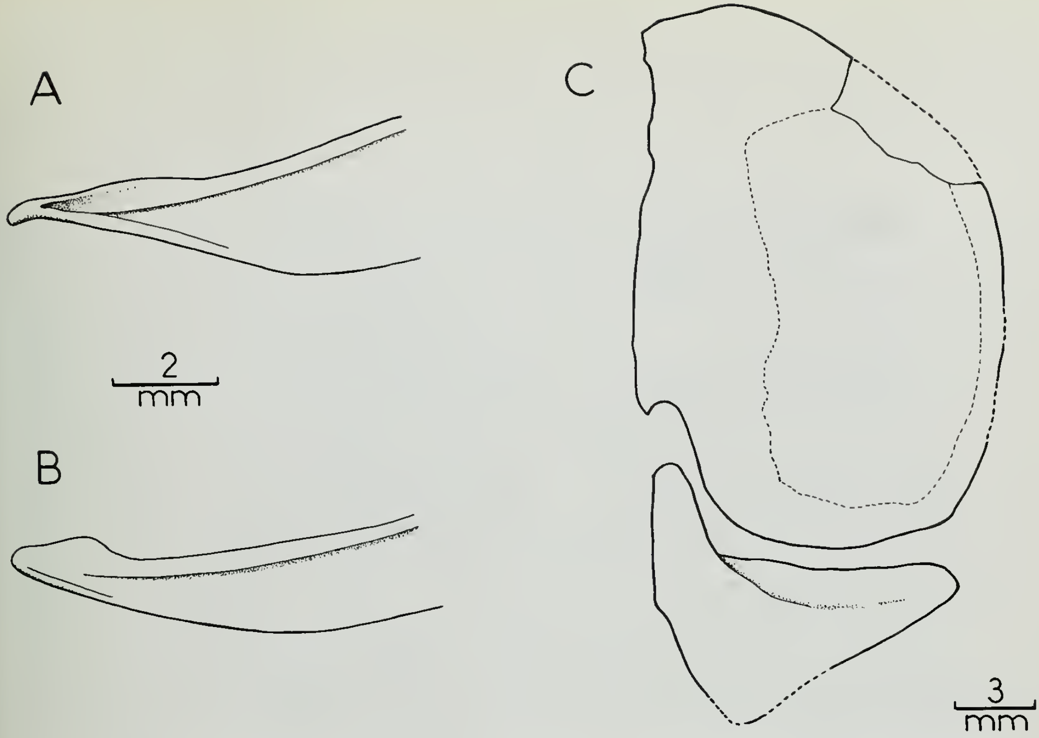

Fig. 10 *Macrosemius rostratus* Agassiz. Lateral views of proximal parts of A, last branchiostegal and B, penultimate branchiostegal in 37094. C, opercular and subopercular of AS.1.640 in lateral view.

The sinuous suture between angular and retroarticular is interrupted by a canal which presumably transmitted the external mandibular ramus of the facial nerve. *Amia* has a similar foramen (Allis 1897 : pl. 20, fig. 6).

The dentary bears about 10 large teeth. Each tooth is laterally compressed and tapers to a point. The teeth are most closely set in the anterior region where the dentary curves sharply towards the mental symphysis. The lateral surface of the dentary is exposed in 37051 (Fig. 4) and 37094. The oral border of the bone rises steeply and forms the greater part of the dermal coronoid process. The open trough for the mandibular sensory canal is very wide and occupies about half of the depth of the dentary below the tooth-row. Three small indentations on the dorsal and ventral margins of the trough may be the remnants of resorbed arches of bone which spanned the canal at an earlier stage of development.

The small surangular occupies the upper posterior part of the coronoid process.

The mandibular sensory canal continued along a large trough in the ventral part of the angular before turning dorsally beneath the quadrate articulation past the remains of another arch of bone. The angular forms a long tapering extension above the sensory canal in the dentary and forms an interdigitating suture with this bone in the medial wall of the canal trough.

The coronoid and prearticular are preserved displaced from the remainder of the mandible in AS.1.639 and AS.1.770 (Fig. 9). The coronoid is short and bears six mammiliform teeth each with a nipple of ganoine. The surfaces of several of these teeth have been worn flat. The two medial teeth, in opposition to the pair of large vomerine teeth, are larger than those forming the outer row. The ventrolateral surface of the coronoid is produced posteriorly to form a short, laterally-compressed process which fitted beneath the dentigerous part of the prearticular.

The prearticular is about twice the length of the coronoid. The dentigerous portion supports about 11 teeth similar in size and shape to those forming the outer row on the coronoid. The

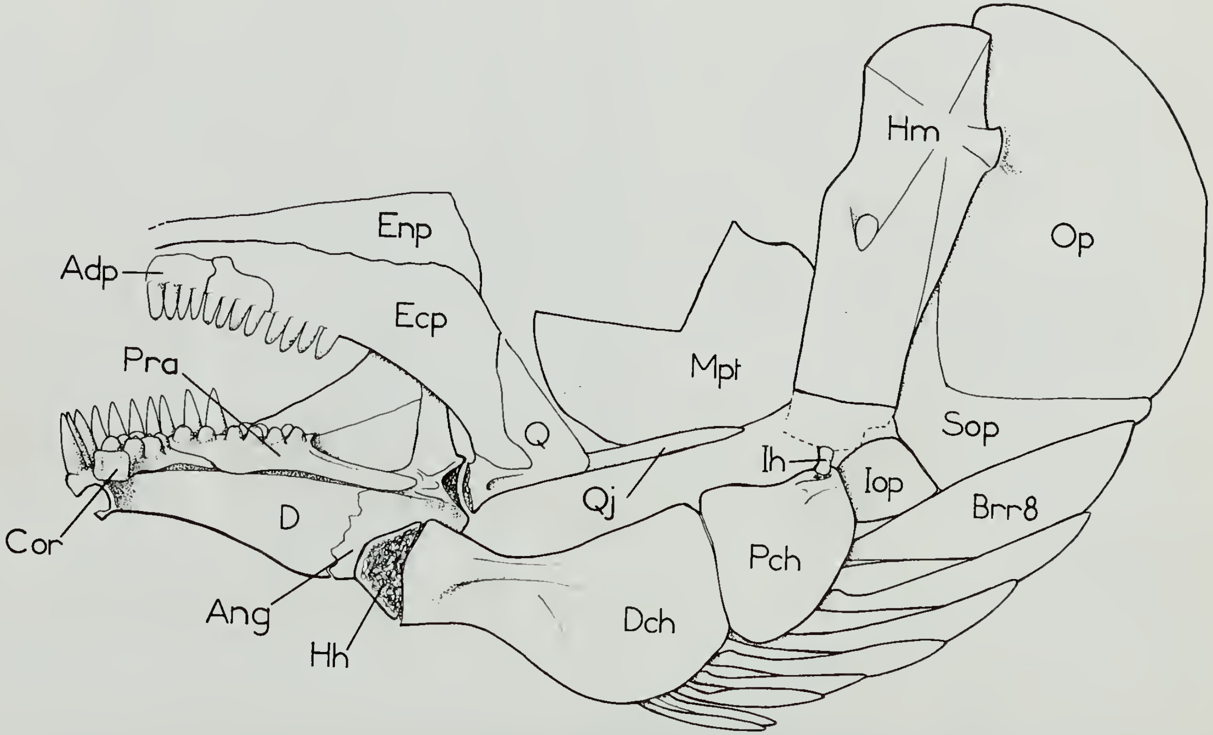

Fig. 11 *Macrosemius rostratus* Agassiz. Restoration of right palate, lower jaw and operculum in medial view. × 3 approx.

anterior two or three teeth form a single row; the remainder form two rows. The ventral surface is grooved for the reception of the posterior process of the coronoid. The prearticular itself forms a long blade-like process posteriorly, inclined slightly ventrally. The ventral surfaces and posterior processes of the two bones rested on the thickened ridge on the inner surface of the dentary. Part of the adductor mandibulae muscle presumably passed into the narrow gap between the dentary and the blade of the prearticular and inserted upon this ridge.

(vii) Preopercular, hyoid arch and branchiostegal series. The preopercular is sharply bent below the level of the orbit; the dorsal and ventral arms form an angle of about 135 degrees. The dorsal arm ends at the level of the opercular process of the hyomandibular and does not reach the skull roof. Its medial surface is closely applied to the hyomandibular (Fig. 13). In contrast to the straight leading edge, the posterior border of the dorsal arm is gently convex. The wide, laterally-compressed sensory canal entered the preopercular dorsally, through a large aperture occupying most of the width of the bone. Within the dorsal arm the canal was exposed by three wide fenestrae. The canal was exposed along its ventral surface along the entire length of the ventral arm. In this region the lateral wall of the canal is deeper than the medial wall.

The opercular (Fig. 10) is deeper than broad. Its trailing edge increases in curvature dorsally. The articulation with the hyomandibular occurs at about one-third of its depth from the dorsal edge. Numerous flat, discrete tubercles of ganoine ornament most of the lateral surface of the opercular. The subopercular is small in comparison with the opercular. Its anterior edge forms an ascending process which abuts against a notch in the latter. Most of the dorsal margin of the subopercular is overlapped laterally by the opercular. A few tubercles of ganoine ornament the bone.

The interopercular is very small, with its anterior end remote from the lower jaw. It forms a straight suture with the subopercular; the remaining edges are rounded.

There are eight branchiostegals, but in one specimen (37094) the lowermost two rays are fused proximally. The uppermost five or six rays are acinaciform and the lowermost two or three

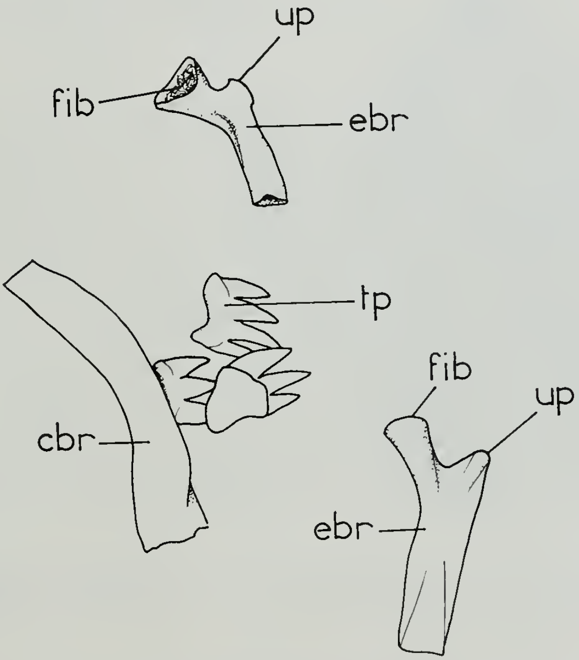

Fig. 12 *Macrosemius rostratus* Agassiz. Scattered parts of the branchial skeleton, as preserved in AS.1.640. × 4 approx.

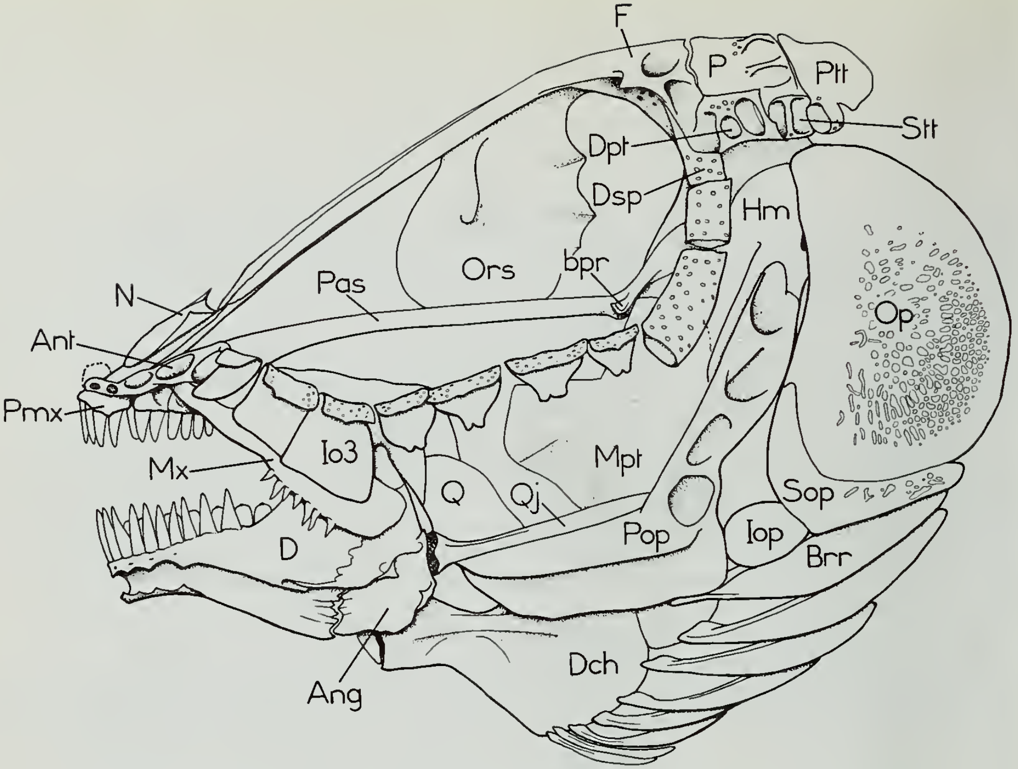

Fig. 13 *Macrosemius rostratus* Agassiz. Restoration of skull. ×2½ approx.

spathiform. The length of the rays decreases rapidly from the top to the bottom of the series. The proximal end of the last (uppermost) ray differs from those of the remainder (Fig. 10); it tapers to a blunt point and is excavated laterally by a deep recess. The dorsal edge of the ray is almost straight. This edge is thickened and curled laterally to form a ventrally-facing groove. This ray does not appear to have articulated with the ceratohyal and was probably fixed to the subopercular. The ventral border of the rays is gently convex. The articulatory heads of the remaining rays form a small dorsal expansion from the thickened upper edge; there is no lateral recess (Fig. 10). The blade of each branchiostegal overlaps that of its ventral successor.

The hyomandibular is described above, together with the palate. The interhyal is very short; it articulated ventrally with a shallow facet close to the posterodorsal corner of the posterior ceratohyal (Figs 6, 11). The distal ceratohyal ossification is short, of little more than twice the length of the posterior ossification, and extends forward to the level of the hind end of the maxilla. The anterior end is slightly expanded and composed of cancellous endochondral bone. Posteriorly the distal ceratohyal forms a very deep, laterally-compressed expansion which articulated with the heads of the branchiostegals. The form of the single hypohyal is not clearly displayed in the specimens.

(viii) Branchial arches. Two epibranchials and a ceratobranchial are preserved, scattered, in specimen AS.1.640 (Fig. 12). The epibranchials are short and slightly bent at about one-third of their length from the articulation with the pharyngobranchial. A short, dorsally-directed uncinate process is also formed at this point.

The ceratobranchial is the usual long, slightly-curved bone. Three small tooth-plates are associated with it, each bearing three or four stout pointed teeth.

Plate 1 *Macrosemius rostratus* Agassiz. Positive print of a radiograph of the skull and pectoral girdle, transfer preparation of 37094. × 3·375.

Plate 2 *Macrosemius rostratus* Agassiz. Positive print of a radiograph, transfer preparation of 37094. × 1·65.

(ix) Vertebral column. Several scattered trunk vertebrae are preserved in AS.1.770. The centra are thick cylinders of bone which constricted the notochord and bear three longitudinal ridges on each lateral surface, defining two deep recesses. The lowermost ridge is continuous with a stout, posteroventrally-directed parapophysis (Fig. 14). It is not clear whether the centrum is entirely perichordal in origin or whether a chordacentral component is also present.

The vertebrae in the posterior part of the body remain unknown, except that paired neural spines are visible at least as far back as the level of the anal fin in a radiograph of 37094 (Pl. 2).

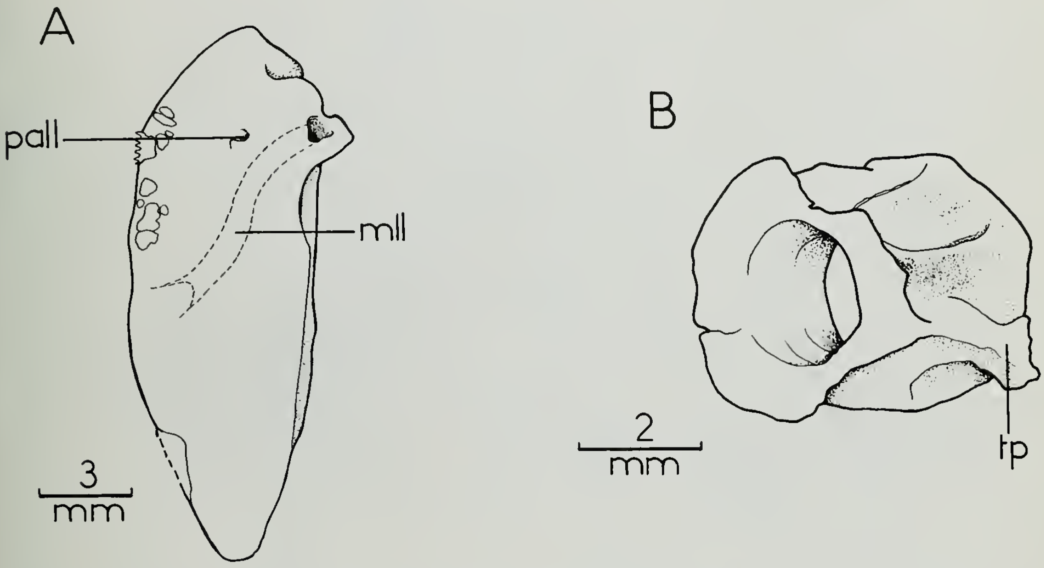

Fig. 14 *Macrosemius rostratus* Agassiz. A, right supracleithrum in lateral view, AS.1.640. **B**, trunk vertebra in anterolateral view, AS.1.770

(x) Pectoral girdle and fin. The left post-temporal is preserved in 37094 (Fig. 5). The triangular laminar portion of the bone tapers towards the midline and is thickened on its ventral surface by a transverse ridge. The lateral margin is inflated to form a short, wide tube around the cephalic part of the main lateral line.

The medial face of the supracleithrum (AS.1.640, Fig. 14) is pierced by the canal of the main lateral line midway along its length. The canal followed an upward sigmoid path through the supracleithrum and emerged through the dorsal part of the leading edge of the bone. The lateral surface bears a pit for a sensory organ posterior to the exit of the sensory canal. A few irregular patches of ganoine occur close to the posterior margin of the supracleithrum; one patch forms serrations along a short length of the margin. The lower part of the bone tapers and overlaps the outer surface of the upper end of the cleithrum.

The cleithrum is preserved in lateral view in AS.1.640 and 37094. The short ventral arm of the bone is inclined downwards forming a wide angle with the dorsal arm. The broad dorsal arm tapers to a point; the lateral surface is shaped to receive the overlap of the supracleithrum. A single vertical row of denticles, each forming three rearwardly-projecting points, extends along the dorsal arm. The lower part of the ventral arm, against which the branchiostegal membrane closed, forms a lateral convexity. The endoskeletal pectoral girdle is not displayed in any of the specimens.

The pectoral fin was supported by about 16 rays associated with six proximal radials (Fig. 15); the cartilaginous distal radials have not been preserved. The first ray is reduced to an unpaired spine. The base of the spine is produced into two lateral, tapering processes for the insertion of the marginal muscle (*sensu* Jessen 1972). The anterior faces of the spine and of the succeeding hemitrich bases are pierced by small, presumably vascular, foramina.

The six proximal radials increase in length posteriorly, with the exception of the fifth, which equals the third in length in 37094. Each radial forms a stout shaft widening slightly towards the extremities. The third and fourth radials are slightly bent in the central region while the same region in the sixth radial bears narrow lateral flanges.

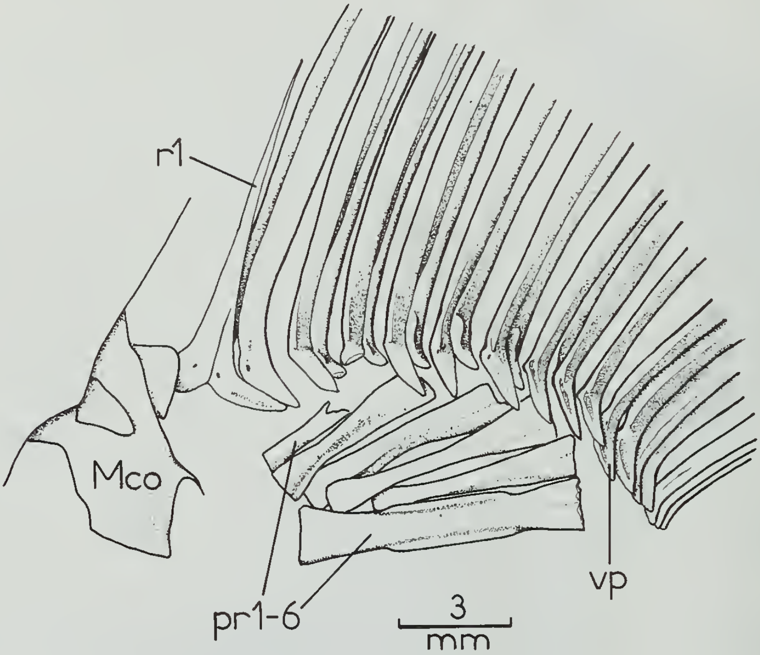

Fig. 15 *Macrosemius rostratus* Agassiz. Base of left pectoral fin in ventral view, as preserved in 37094.

(xi) Pelvic fin. The basipterygium resembles that of *Amia* (Fig. 16). The wide, dorsoventrally-compressed anterior expansion tapers gradually backwards, expanding sharply to form the articular surface. The radials are not exposed in the specimens. The pelvic fin consists of six rays. The base of the leading ray is preceded by four very small splints of bone, the larger two forming a pair. These splints are probably reduced basal fulcra. All the pelvic rays except the first are segmented and branched. The bases of the ventral hemitrichia are produced laterally to form processes for the insertion of the fin inclinator muscles; the length of these processes decreases posteriorly.

(xii) Anal and dorsal fins. The anal fin is large and rounded, with the rays widely spaced and approximately parallel. There are seven rays, each articulating with a long slender radial (37094, Fig. 17). Each hemitrich forms a lateral process at its base for the insertion of the inclinator muscles, as is usual. The leading, unbranched ray is shorter than the unsegmented proximal region of the second ray. The leading ray is preceded by a long, unpaired, asymmetrical splint, and by a pair of shorter splints.

The number of dorsal fin-rays varies between 32 and 39; the dorsal fin-ray counts of six specimens are as follows. 4453 : 32; 1901.67.1 : 38; AS.6.24 : 39; 1954.1.530 : 32; 1904.1.18 : 38; Ei : 37; Ei : 39. The fin extends from the rear of the skull to the base of the axial lobe of the caudal fin. The endoskeletal supports equal the rays in number. Two or three closely-set splints lie in front of the leading ray; these are reduced basal fulcra. No fringing fulcra are present. All the rays branch at least twice; those in the posterior third of the fin branch three times. The fin-rays

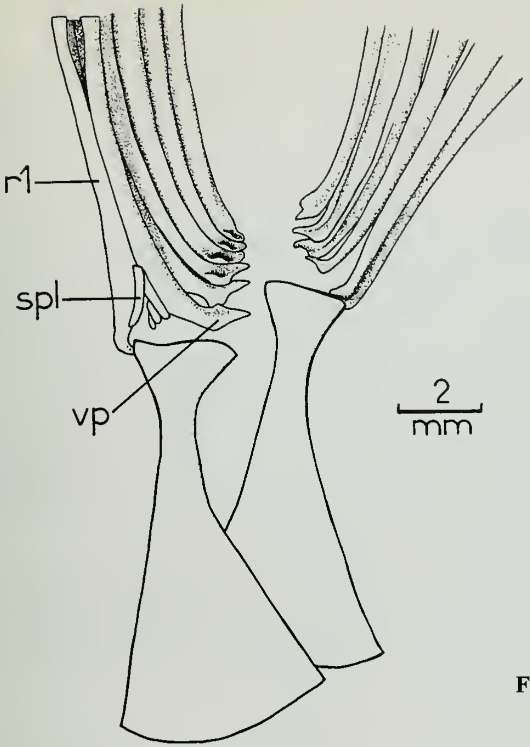

Fig. 16 *Macrosemius rostratus* Agassiz. Pelvic fins and girdles in ventral view, as preserved in 37094.

thicken in lateral profile in the caudal region, where the rays become more closely-set. The dorsal and caudal fin-rays display an unusual feature: the segments of each ray bear one short, dorsally-inclined ganoine spine along the posterolateral surface (Fig. 18); these spines continue onto the unsegmented ray bases.

The distal radials of the fin were presumably of cartilage and are not preserved. Each middle radial segment is inclined backwards (Fig. 18); it is preserved as a thin-walled tube of perichondral bone, irregularly constricted in the centre and pierced by a vascular foramen. The proximal segment is dagger-shaped and flares dorsally to form a thin-walled cone which bore the articulatory surface for the middle segment. A thin flange extends along the lateral surfaces of the proximal radial segment, separating the areas of origin of the elevator and depressor ray muscles. A vascular foramen pierces the base of the cone anterior to the flange.

As usual the radials are arranged so that each ray articulated with both the distal segment of its own radial and with the proximal segment of the succeeding radial.

(xiii) Caudal fin. The number of caudal fin-rays varies between 11 and 13, of which eight originate beneath the axial lobe. The caudal axial skeleton remains unknown. The uppermost ray, supporting a series of fringing fulcra, forms a continuation of the longest axial lobe scale-row, with no sharp demarcation between the two; the base of this ray does not penetrate beneath the squamation (Fig. 19). The remaining axial lobe rays pass beneath the scales and clasp the upper hypurals. The bases of the eight rays originating below the axial lobe clasp only the tips of their endoskeletal supports. The caudal fin is rounded, and only about one-third of its area is supported by the axial lobe rays.

The ventral surface of the caudal peduncle bears four massive basal fulcra, their edges straight and converging to a sharp point. The series is continued along the lowermost fin-ray by paired fringing fulcra which rapidly decrease in size towards the rear of the fin.

(xiv) Squamation. The squamation of *Macrosemius* diplays two features of special interest. Perhaps most striking is the total absence of scales in a strip lying on either side of the dorsal fin, occupying from one-third to a quarter of the depth of the trunk. The squamation of this genus is further characterized by the presence of secondary scale rows which intervene between the transverse rows of the trunk in the region above the first longitudinal scale row dorsal to the lateral line. This scale-pattern is described in *M. fourneti*, below, in which the arrangement of the scales is more surely known.

Below the lateral line the scales form a regular pattern of rectangles. These have been described in a young individual (P7177) by Schultze (1966 : 275, fig. 30). In the anterior region, ganoine is restricted to the denticles on the trailing edge of the scales. The bony layer is crossed by fine radial markings on the anterior half of each scale, and by concentric lines posteriorly. The ganoine-covered area of the scales increases in the caudal region, forming irregular patches. The abdominal scales of an older specimen are displayed in both lateral and medial view in AS.1.640. Here the ganoine layer is complete except for a narrow strip close to the anterior margin; the surface of the ganoine is smooth. Internally the scales forming the transverse rows are linked by small pegs-and-sockets. The shallow internal rib is inclined slightly in advance of the peg-and-socket. Schultze (1966 : fig. 16b) has drawn a lateral line scale in medial view. The sensory canal entered the anterior border of the scale close to the dorsal edge and continued through a thin-walled tube (collapsed in the specimen) which opens midway across the scale and continues as a narrow groove. A small pore, which presumably transmitted the sensory nerve, pierces the wall of the tube.

Three large circumanal scales are preserved in 37094. The anterior pair, which flanked the anus, are roughly oval in shape. They are followed by a large, median saddle-shaped scale immediately preceding the anal fin. All three scales have rounded edges and are devoid of denticles.

The postcleithral scales are nowhere clearly visible. The uppermost, much deeper than wide, is partially visible in some specimens, for example 37094.

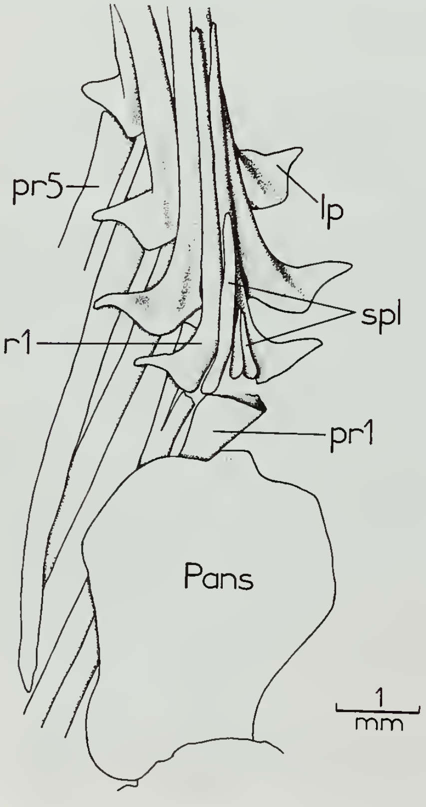

Fig. 17 *Macrosemius rostratus* Agassiz. Base of anal fin in anteroventral view, as preserved in 37094.

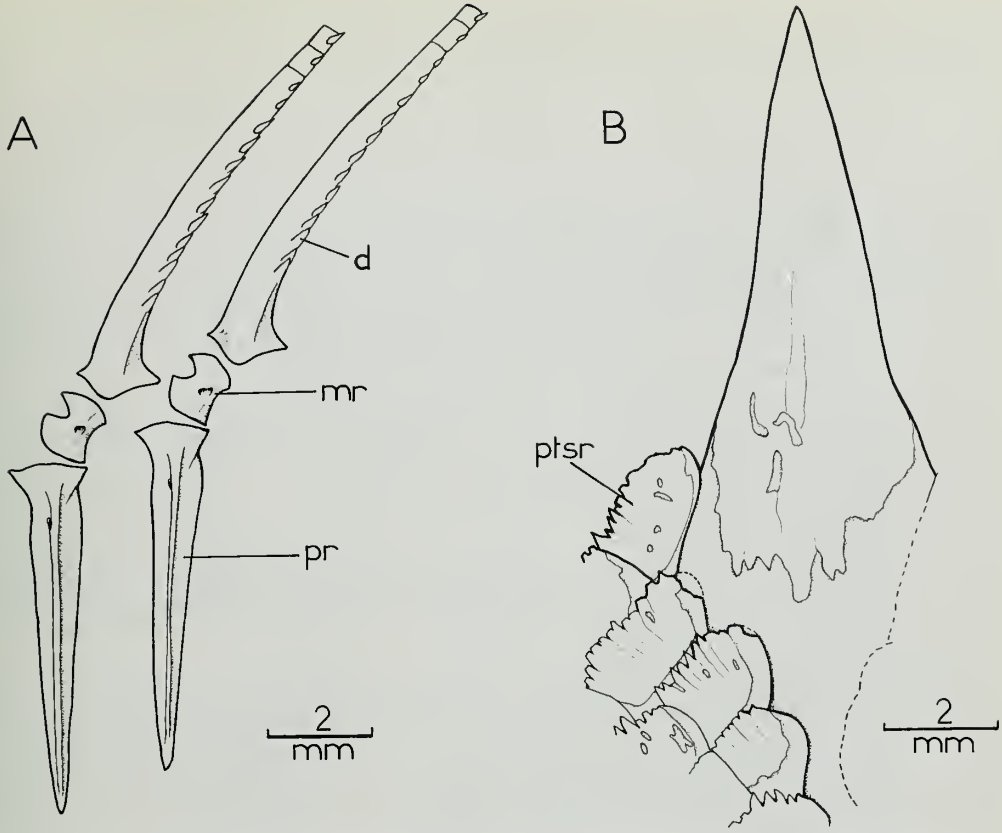

Fig. 18 *Macrosemius rostratus* Agassiz. A, lateral view of two dorsal fin-rays and their supports. B, anterior ventral basal fulcrum on caudal peduncle. 37094.

Macrosemius fourneti (Thiollière 1850)

Fig. 19

1850 *Disticholepis fourneti* Thiollière : 136.
1854 *Disticholepis fourneti* Thiollière; Thiollière : pl. 7.
1858 *Disticholepis dumortieri* Thiollière : 783.
1860 *Disticholepis fourneti* Thiollière; Wagner : 402.
1873 *Disticholepis fourneti* Thiollière; Thiollière : 15.
1873 *Disticholepis dumortieri* Thiollière; Thiollière : 15; pl. 6, fig. 1.
1873 *Macrosemius rostratus* Agassiz; Thiollière : pl. 5, fig. 2.
1883 *Disticholepis dumortieri* Thiollière; Sauvage : 479.
1887 *Macrosemius fourneti* (Thiollière) Zittel : 218.
1895 *Macrosemius fourneti* (Thiollière); Woodward : 178.
1895 *Macrosemius dumortieri* (Thiollière) Woodward : 178.
1914 *Macrosemius fourneti* (Thiollière); Eastman : 365.
1914 *Macrosemius dumortieri* (Thiollière); Eastman : 365.
1949 *Disticholepis fourneti* Thiollière; Saint-Seine : 201; pl. 21a; text-fig. 88–9.
1949 *Disticholepis dumortieri* Thiollière; Saint-Seine : 204; pl. 21b.
1949 *Macrosemius rostratus* Agassiz; Saint-Seine : 199; pl. 23d; text-fig. 87.

DIAGNOSIS. *Macrosemius* with between 33 and 35 dorsal fin-rays, with the mode at 34; the large basal fulcra along the ventral border of the caudal peduncle possessing convex edges; supraorbitals present.

Holotype. Muséum d'Histoire Naturelle, Lyon, 15.237; from Cerin (Ain, France).

Horizon and Localities. Lower Kimmeridgian of Cerin.

Material. BM(NH): P1091, P4684–5; specimens in the Muséum d'Histoire Naturelle, Lyon (see Saint-Seine 1949 for registration numbers). None was available for acetic acid preparation.

Remarks. Thiollière (1858, 1873) and later Saint-Seine (1949) described the following species in their works on the Lower Kimmeridgian fish fauna of Cerin: *Macrosemius rostratus* Agassiz, *Macrosemius helenae* Thiollière, *Disticholepis fourneti* Thiollière and *D. dumortieri* Thiollière. *Disticholepis* strongly resembles *Macrosemius.* However, both authors took *M. helenae* to be typical of the latter genus and considered that the specimens of *Disticholepis* were sufficiently dissimilar to justify the erection of the new genus. *M. helenae* and *Disticholepis* are indeed very different, since in fact the former was wrongly placed in the genus *Macrosemius.* Both Thiollière and Saint-Seine believed that the dorsal fin of *M. helenae* was single; it is, however, divided, and in the present study this species has been transferred to *Notagogus.*

Thus, following Zittel (1887) and Woodward (1895), *Disticholepis* is synonymized with *Macrosemius.* As Saint-Seine (1949 : 404) says, *M. fourneti* and *M. dumortieri* are very similar; they are considered here to be conspecific. The specimens from Cerin hitherto referred to *M. rostratus* are not known in enough detail to be separated from *M. fourneti.*

Saint-Seine's (1949 : 199–204) interpretation of the material of *M. fourneti* is reassessed below by comparison with the type species.

Description. (i) Skull roof and braincase. The drawing given by Saint-Seine (1949 : fig. 87) under the name of *M. rostratus* (15.229) is inaccurate; the bones of the skull roof are crushed and their outlines difficult to discern. There is no evidence that the supraorbital sensory canal followed the course given in the figure.

The skull roof is displayed in lateral view in 15.235 and 15.226; it is very similar to that of *M. rostratus.* Saint-Seine (1949 : 202) discusses several peculiarities of the skull roof. The 'hiatus' he describes between the frontal and parietal is probably due to the post-mortem separation of the non-overlapping suture between the two bones, and was not present in life as he suggests. The fenestrae in the supratemporal commissure, described in *M. rostratus* above, he interprets as 'une rangée de cuvettes très plates separées par des piliers en relief'; he considered these to be distinct

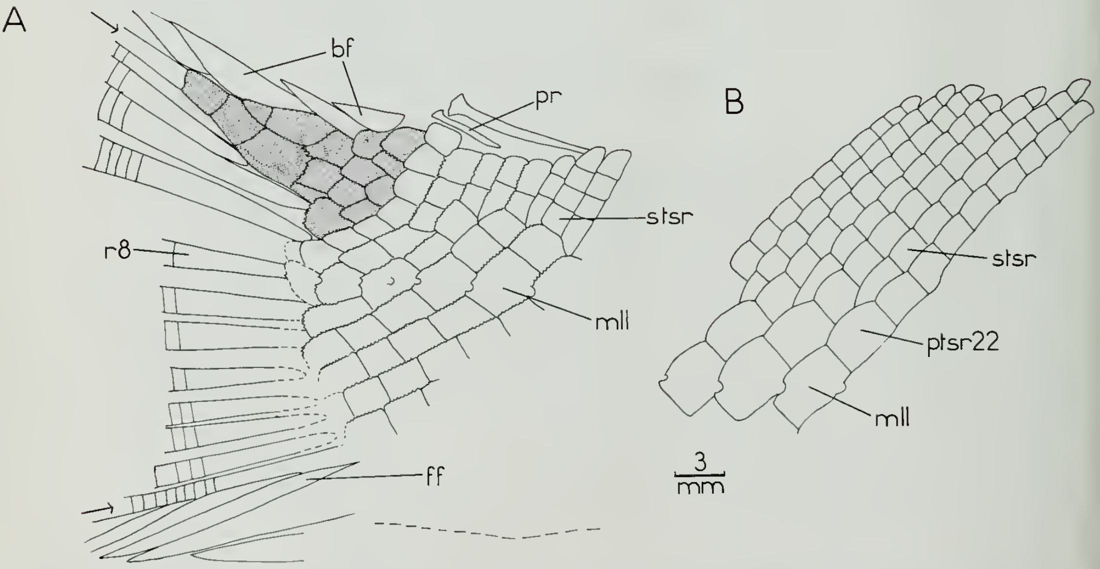

Fig. 19 *Macrosemius fourneti* Thiollière. Squamation, as preserved in impression in P4685. A, caudal region, axial lobe shaded. B, abdominal region, above main lateral line.

from the commissure which he supposed crossed close to the anterior border of the parietal (1949 : fig. 88–89). There is no evidence to support this position for the commissure. Saint-Seine correctly notes the reduced size of the supratemporal. The dermopterotic and frontal too are similar to those of *M. rostratus*.

In contrast to *M. rostratus*, *M. fourneti* has a row of four supraorbitals along the lateral embayments of the frontals (Saint-Seine 1949 : 202).

(ii) The infraorbital series. The dermosphenotic resembles that of the type species. Two of the infraorbitals are identified by Saint-Seine in the preorbital region (1949 : fig. 88–89). The remaining bones of the head are too badly crushed for a useful description to be given. The few structures which are clearly visible resemble those of *M. rostratus*; eight branchiostegals are preserved in 15.289 and the stout rounded teeth of the palatine and splenial bones are visible in 15.226. As in the type species, the opercular is ornamented with discrete tubercles of ganoine (15.226).

(iii) Paired fins. These are exposed in 15.229. As in *M. rostratus* the pectoral fin is preceded by a spine-like ray and the pelvic fin by reduced basal fulcra. Fringing fulcra are absent on both fins.

(iv) Anal and dorsal fins. The anal fin resembles that of the type species. The number of dorsal fin-rays varies between 33 and 35, with the mode at 34. The dorsal fin-ray counts of five specimens are as follows. 15.219 : 34; 15.235 : 34; 15.229 : 33; 15.222 : 34; 15.237 : 35. This contrasts with the larger range of 32–39 displayed by *M. rostratus*. The variation in fin-ray structure along the length of the dorsal fin was noted by Thiollière (1873 : 14). As in the type species the rays in the posterior part of the fin become broader, presenting a larger lateral surface area. Also the unsegmented bases are shorter in the caudal region. The denticles along the fin-rays clearly originate from the tubercles of ganoine on the posterolateral surface of each ray segment.

(v) Squamation. The squamation of the dorsal region of the trunk is clearly discernible in impression in P4685 (Fig. 19). The area along either side of the dorsal fin is completely free from scales. The lateral line scales are the deepest, and number about 40; a few bear pits of the accessory lateral line. As in *M. rostratus*, secondary scale rows occur between the transverse rows. The most anterior of these secondary rows, comprising three or four scales, appears most often behind the twelfth or thirteenth transverse row counting from the head. There follows an interval of several rows before increasingly longer secondary rows interpose between all subsequent rows before the caudal fin. The secondary rows extend ventrally to reach the longitudinal scale row above the lateral line. The scales of the regular transverse rows are narrowed to equal the width of the secondary rows adjacent to them.

The axial lobe of the caudal fin, as defined by the 'reversed' squamation, is small (Fig. 19); this may be correlated with the fact that few (3–5) of the caudal fin-rays originate from the lobe compared with the number of rays which emerge below it (8, as in all macrosemiids). The axial lobe squamation of *Macrosemius* consists of about four disorganized rows; the longest, with about six scales, continues as the hemitrich of the uppermost caudal fin-ray, and the remaining rows terminate dorsally as basal fulcra.

Genus *LEGNONOTUS* Egerton 1854

Diagnosis. Small macrosemiid fishes, the trunk tapering gradually to form a broad caudal peduncle; skull roof bearing ganoine; gape small, the quadrate articulation lying beneath the anterior part of the orbit; dentigerous expansion of maxilla with upper and lower borders straight and diverging posteriorly, hind border also straight and perpendicular to oral border, bearing about 13 small, closely-set teeth; mandible with dentary bearing about 12 closely-set teeth, coronoid teeth rounded; leading edge of preopercular forming sharp angle; abdominal vertebrae forming thin cylinders, notochord unconstricted; pectoral fin with about 15 rays, leading ray reduced to unpaired splint, no fringing fulcra; pelvic fin formed by five rays preceded by basal and fringing fulcra; anal fin with seven rays, base compact; caudal fin weakly forked, axial lobe bearing five rays; dorsal fin single and long, preceded by basal and fringing fulcra, outline high anteriorly, convex posteriorly; region immediately on either side of dorsal fin devoid of scales; scales rhomboid.

TYPE SPECIES. *Legnonotus cothamensis* Egerton 1854.

INTRODUCTION. The genus *Legnonotus* was founded by Egerton (1854) to include a small fish with an elongated dorsal fin, *L. cothamensis*, from the Rhaetic of Gloucestershire. Later Woodward (catalogue MS) intended to transfer Gorjanovic-Kramberger's (1905) specimens of *Ophiopsis attenuata* Wagner, from the Upper Trias of Hallein (Austria), to a new species of this genus, *L. krambergeri*; this manuscript name is now given formal status. The latter species is described first since it is the better known of the two.

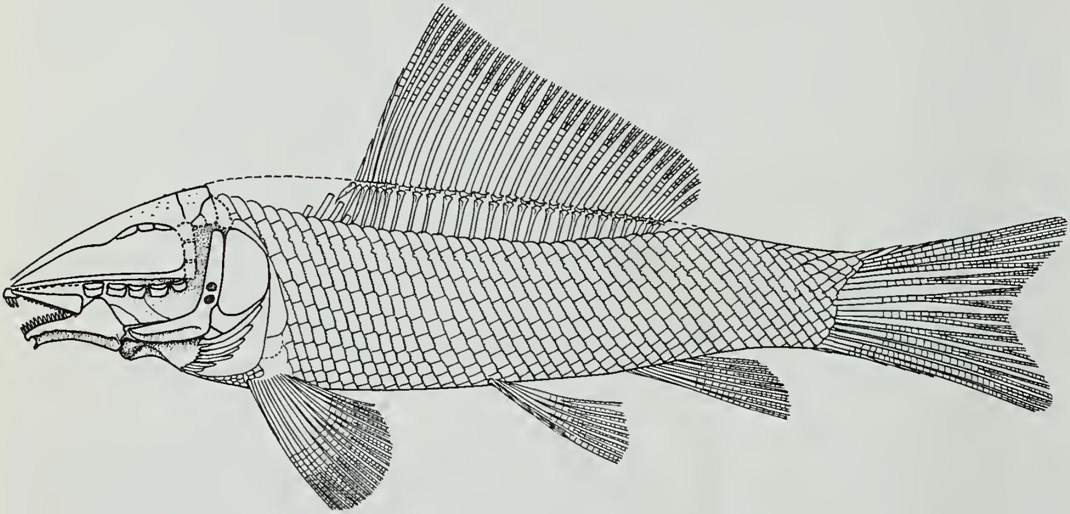

Fig. 20 *Legnonotus krambergeri* sp. nov. Restoration of skeleton. ×2½ approx.

Legnonotus krambergeri sp. nov.

Fig. 20

1905 *Ophiopsis attenuata* Wagner; Gorjanovic-Kramberger : 218; pl. 20, figs 3, 4.

DIAGNOSIS. *Legnonotus* with about 25 dorsal fin-rays; dentary teeth tall and sharp.

HOLOTYPE. British Museum (Natural History) P10287, from the Upper Trias of Hallein, Austria.

HORIZON AND LOCALITY. Upper Trias of Hallein, Austria.

MATERIAL. BM(NH): P10287, P10286; Leo: 75, 88, 93, 98, 108.

REMARKS. The small jaws, lack of a gular and supramaxilla and the form of the infraorbitals in this genus all indicate that these fishes belong to the Macrosemiidae *s. str.* and not to *Ophiopsis*. They are ascribed to the poorly-known genus *Legnonotus* on account of the long, single dorsal fin and the forked tail.

DESCRIPTION. (i) General features. *Legnonotus krambergeri* is a small elongate fish reaching a standard length of 65 mm (Fig. 20).

(ii) Skull roof and braincase. The skull roof is poorly preserved in the specimens; it is best seen in specimens 93 and 108. The parietals are ornamented with small, regularly dispersed tubercles of ganoine. Their greatest width is along the frontoparietal suture, which is gently convex anteriorly. The lateral border of the parietal is embayed posteriorly where it formed contact with the supratemporal (88). The supratemporal commissure is not visible.

The frontals have the usual macrosemiid form, with a long slender preorbital region and a short, broad postorbital region. As usual, the supraorbital sensory canal runs close to the posterior edge of the orbital embayment before turning medially to pass alongside the straight interfrontal suture. As in *Macrosemius* the canal lay in a trough formed by the frontals in the preorbital region. The ganoine ornament on the posterior part of the frontal is preserved in impression in specimen 88; the ganoine tubercles are aligned in rows parallel to the midline. In 93, the ganoine forms complete ridges. The remaining bones of the skull roof are unknown.

(iii) Circumorbital bones. Three supraorbitals lie in the orbital embayment of the frontal. Their surface is ornamented with a few discrete tubercles of ganoine. Traces of four infraorbitals are visible in specimen 108; these are probably the 4th–7th of the series, and appear to resemble those of the type genus. The dermosphenotic is not preserved.

(iv) Dermal upper jaw. The maxilla is preserved in impression in specimens 93 and 108. The dorsal and oral borders are straight, and diverge posteriorly. The latter bears a long row of about 13 very small teeth. The hind border is also straight, and is perpendicular to the lower.

(v) Lower jaw. The dentary bears a row of about 12 tall, pointed, closely-set teeth. Although the bones of the lower jaw are crushed beyond recognition, enough is visible in specimen 93 to show that, as in other members of the family, the mandibular sensory canal ran in an open groove along the ventral border. The jaw articulation lies below the anterior part of the orbit. Several coronoid teeth, their apices worn flat, are visible in the same specimen.

(vi) Preopercular and opercular series. What little of the preopercular can be seen in the specimens indicates that this bone was sharply bent as in *Macrosemius*. The opercular series is best preserved in specimen 93. The opercular is somewhat wider in proportion to its depth than it is in the type genus. The branchiostegals display a marked reduction in length and depth passing down the series. The distal ceratohyal is preserved in impression in 108; as in other macrosemiids the proximal end is stout, expanding to form a deep, laterally-compressed expansion posteriorly.

(vii) Vertebral column. Abdominal centra are exposed in 93, although they are too poorly preserved for an accurate description to be given. Six supraneurals are visible behind the skull in P10286 and 93, as in *Macrosemius*.

(viii) Pectoral fin. The pectoral fin was supported by about 15 rays preceded by an unpaired spine, probably a modified ray as in the type genus. There are no fringing fulcra.

(ix) Pelvic fin. The pelvic fin consists of five rays; the leading ray is preceded by about four basal fulcra and two pairs of fringing fulcra.

(x) Dorsal and anal fins. The dorsal fin consists of about 25 rays. As in *Macrosemius*, the fin is undivided. The anterior rays are the tallest, the remainder decreasing in height to form a gently concave border. Seven basal fulcra and several pairs of fringing fulcra are present. The radials are similar to those of the type genus.

The anal fin consists of seven rays; their bases are crowded more closely together than those of *Macrosemius*.

(xi) Caudal fin. The outline of the fin is weakly forked. Five rays emanate from the axial lobe and eight, as usual, from below the lobe. Both upper and lower edges bear basal and fringing fulcra.

(xii) Squamation. *Legnonotus* shares with *Macrosemius* the absence of scales along a strip on either side of the dorsal fin. The lateral line, passing through about 37 deep, rhomboid scales, is placed in an unusually high position along the body. Unlike the condition in the type genus, no secondary transverse scale-rows occur.

Legnonotus cothamensis Egerton 1854

1854 *Legnonotus cothamensis* Egerton : 435.
1855 *Legnonotus cothamensis* Egerton; Egerton : 4; pl. 7, figs 9–12.
1895 *Legnonotus cothamensis* Egerton; Woodward : 176.
1966 *Legnonotus cothamensis* Egerton; Schultze : 274, text-fig. 29.

DIAGNOSIS. *Legnonotus* with about 30 dorsal fin-rays; dentary teeth blunt.

HOLOTYPE. Specimen in the Bristol Museum.

Horizon and Locality. Rhaetic (Cotham Marble) of Aust Cliff, Gloucestershire, England.

Material. BM(NH): P1092, three pieces of matrix containing scattered fragments, of which one was prepared in dilute acetic acid.

Description. Unfortunately the bones in the BM(NH) material are largely fragmented. The only bone which can certainly be identified as part of a macrosemiid is a right dentary. The remaining fragments, mainly of scales and vertebrae, may belong to the other fish found in the Cotham Marble, *Pholidophorus higginsi* (Egerton 1855). The centra present consist of rings of dense bone to which the cancellous cartilage-bone of the arches and transverse processes are attached. These are closely similar to the centra of *Ichthyokentema* (Griffith & Patterson 1963) and are unlikely to belong to *Legnonotus*. Similar doubt applies to the identity of the deep trunk scales drawn by Schultze (1966 : fig. 29).

Genus *ENCHELYOLEPIS* Woodward 1918

Diagnosis. Very small macrosemiid fishes, trunk gradually tapering from the occiput backwards; head large; dentary teeth closely set and pointed; abdominal centra annular, neural and haemal arches short and stout; about five pelvic fin-rays; dorsal fin long, undivided, with about 25 rays articulating upon stout radials; seven anal fin-rays; caudal fin rounded; scales cycloid, overlapping.

Type species. *Macrosemius andrewsi* Woodward (1895a).

Introduction. Sauvage (1883) described a very small macrosemiid from the Upper Portlandian of Meuse (France), *Macrosemius pectoralis*. Woodward (1895a) described another similar species, *M. andrewsi*, from the English Purbeck. In his revision of the Wealden and Purbeck fishes, Woodward (1918) transferred these two species to a new genus, *Enchelyolepis*.

Remarks. Woodward's description of the two specimens known of this genus is adequate. However, the specimens are important in that they display the endoskeleton of the caudal fin; this remains unknown in other macrosemiids. A redescription of this important region is given below.

Enchelyolepis pectoralis (Sauvage 1883)

Fig. 21

1883 *Macrosemius pectoralis* Sauvage : 477; pl. 12, fig. 17.
1895 *Macrosemius pectoralis* Sauvage; Woodward : 179.
1918 *Enchelyolepis pectoralis* (Sauvage) Woodward : 81; pl. 17, fig. 7.
1966 *Enchelyolepis pectoralis* (Sauvage); Schultze : 276; text-fig. 34.

Diagnosis. *Enchelyolepis* with very broad, laterally-compressed neural arches and spines.

Holotype (and only specimen). BM(NH): P7359.

Horizon and Locality. Upper Portlandian of Savonnières-en-Perthois, Meuse, France.

Description. See Woodward 1918 : 81; pl. 17, fig. 7. Much of the internal skeleton of the caudal fin in this specimen is preserved in impression (Fig. 21). Four rays emerge from the axial lobe of the fin, and only five branched rays occur below this, preceded by three short, unsegmented rays. Since all other adult macrosemiids possess eight segmented lower rays, the three unsegmented lower rays have probably not reached their adult length. In young specimens of *Notagogus pentlandi* Agassiz too, only five or six of the lower rays are long and segmented; there are eight in the adult. The lower rays articulated upon six axial supports of which two have survived in the specimen (the rest have left impressions); they form stout cylindrical rods. Since the haemal arches in this region are not preserved, there is nothing to indicate which of these are hypurals.

The epaxial region of the fin is traversed by one short and four elongated elements; the last two of these articulated with the dorsal basal fulcra. Woodward (1918 : 81) identified them as neural arches, but in the specimen of *E. andrewsi* (P6303), in which these bones are entirely preserved, they are unpaired and are thus neural spines or epurals. In fact all these elements except the third are free from their neural arches and are thus epurals. The small ural neural arches, traces of which

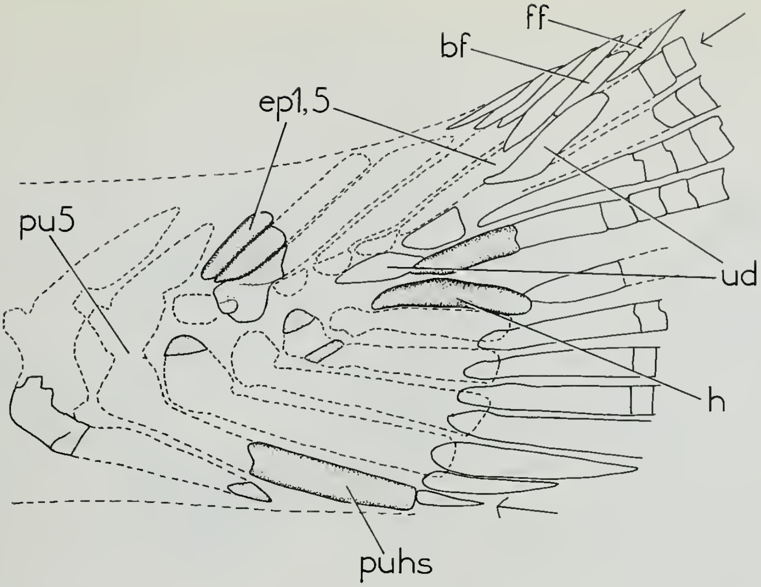

Fig. 21 *Enchelyolepis pectoralis* (Sauvage). Caudal fin, as preserved in P7359; the dashed lines denote impressions in the matrix. × 12.

remain, were not elongated. Three urodermals, remnants of the rhomboid squamation of the axial lobe, are also preserved.

The trunk scales are, remarkably, cycloid. Schultze (1966 : 276, text-fig. 34) has drawn three of them and noted their similarity with those of *Amia* in the radial markings on the anterior overlapped region.

Enchelyolepis andrewsi (Woodward 1895a)

1895a	*Macrosemius andrewsi* Woodward : 148; pl. 7, fig. 3.
1895	*Macrosemius andrewsi* Woodward; Woodward : 180.
1918	*Enchelyolepis andrewsi* (Woodward) Woodward : 80; pl. 17, fig. 6.

Diagnosis. *Enchelyolepis* with more slender haemal arches and neural spines than those of *E. pectoralis.*

Holotype (and only specimen). BM(NH): P6303.

Horizon and Locality. Middle Purbeck of Teffont, Wiltshire, England.

Description. See Woodward 1918 : 80; pl. 17, fig. 6.

Genus *PROPTERUS* Agassiz 1834

Diagnosis. Small to medium-sized macrosemiid fishes; trunk somewhat deepened and irregularly fusiform with the dorsal profile slightly bent at the level of the first dorsal fin-ray; supratemporals reduced; supratemporal commissure largely surrounded by parietals, whose surfaces are raised into strong ridges bearing ganoine; frontoparietal suture serrate; cranial division of main lateral line exposed by large fenestrae in dermopterotic; vomers bearing a single row of tall, pointed teeth; ventral parts of first three infraorbitals overlapping the maxilla; gape very small, the jaw articulation lying anterior to the orbit; premaxillary teeth tall and pointed; dentigerous expansion of maxilla symmetrical, the upper and lower edges straight, diverging, the hind border convex, teeth greatly reduced in size and number; mandible with closely-set teeth on dentary, medial wall of sensory canal trough in articular perforated by small pores; lateral border of palate rising steeply from jaw articulation; anterodorsal edge of metapterygoid forming an obtuse angle; leading edge of preopercular following a smooth curve; opercular ornamented with small tubercles of ganoine, uppermost branchiostegal ray devoid of ganoine; single vertical row of denticles on cleithrum; vertebral centra, in form of dorsal crescents, restricted to predorsal region of notochord; pectoral fin with about 16 rays and six proximal radials, hemitrichia of leading ray incompletely fused together, fringing fulcra absent; pelvic fin comprising six rays preceded by basal and fringing fulcra; base of anal fin compact, leading ray extending below caudal fin, preceded by basal and fringing fulcra; dorsal fin divided with at least some rays of the anterior part taller than those of the posterior part; caudal fin deeply forked, with between six and eight rays on the axial lobe, fringing fulcra on both borders; squamation entire, regular, lateral trunk scales deeper than broad, posterior edge slightly convex, anterior ventral scales cycloid.

TYPE SPECIES. *Propterus microstomus* Agassiz 1834.

INTRODUCTION. The genus *Propterus* was erected by Agassiz (1834) to include a single species from the Lower Kimmeridgian of Bavaria, *P. microstomus*. Wagner (1851, 1863) added *P. gracilis*, *P. speciosus* and *P. elongatus* from the same locality.

Woodward (1895) transferred Costa's (1850) *Rhynchoncodes scacchi*, from the Lower Cretaceous of Castellamare near Naples, to *Propterus*. Also, he considered *P. gracilis* and *Notagogus zieteni* (Agassiz 1835) to be synonymous with *P. microstomus*. Sauvage (1903) described *P. vidali* from the Neocomian of Lerida, Spain, and Eastman (1914a) recorded a new species from Bavaria, *P. conidens*. More recently Vianna (1949) recorded a specimen of *P. microstomus* from the Lusitanian of Portugal.

REMARKS. Wagner (1851) gave a short description of *P. speciosus*. Since his specimen appears to differ from Agassiz's *P. microstomus* only in its larger size, it is here taken to belong to Agassiz's species.

Woodward (1895) referred several specimens in the British Museum to *P. speciosus*. However, the anterior dorsal fin of these specimens is tall throughout its length; in contrast the very long anterior dorsal fin-rays of *P. speciosus* decline rapidly in height to produce a falcate fin. Examination of the type specimen of *P. elongatus* (Wagner 1863) reveals that in this species too the anterior dorsal fin shows no great variation in height along its length, although Wagner did not mention this in his description and gave no drawing of the specimen. Woodward's specimens agree with *P. elongatus* in their proportions as well as in the shape of the dorsal fin, and are thus referred to this species here.

Eastman (1914a) followed Woodward in assigning the Carnegie Museum specimens to *P. speciosus*; these too belong to *P. elongatus*. Also, *P. conidens* Eastman is indistinguishable from *P. microstomus*.

P. elongatus will be described first since this is the best known species.

Propterus elongatus Wagner 1863

Pls 3–4; Figs 22–30

1863 *Propterus elongatus* Wagner : 645.
1881 *Notagogus macropterus* Vetter : 46.
1881 *Histionotus parvus* Vetter : 48; pl. 2, fig. 5.
1895 *Propterus speciosus* Wagner; Woodward : 184, pl. 3, fig. 5.
1914a *Propterus speciosus* Wagner; Eastman : 407, pl. 13, fig. 1.

DIAGNOSIS. *Propterus* reaching standard length of 130 mm; mean proportions as percentages of standard length: head length 34%, trunk depth 36%, predorsal length 42%, prepelvic length 58%, preanal length 79%; fin-ray counts: D(ant.) 14–16, D(post.) 14–16, P 17, V 6, A 5, C 14–15; about 37 lateral line scales; scales thin with large serrations; two lobes of dorsal fin very close together; outline of anterior dorsal convex; fulcra absent from posterior dorsal; caudal fin-rays bifurcating a maximum of twice.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.1.767.

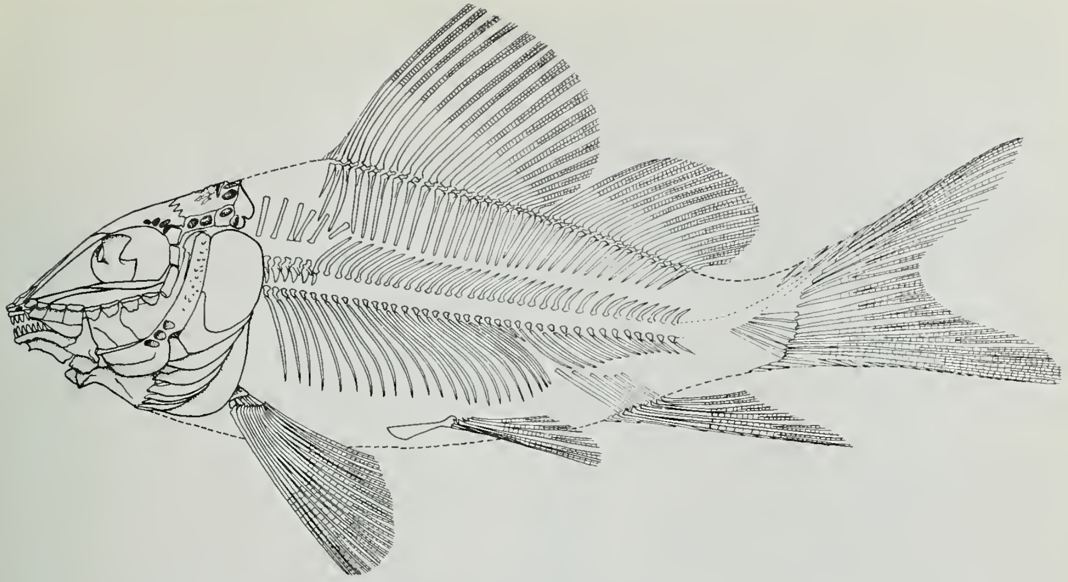

Fig. 22 *Propterus elongatus* Wagner. Restoration of skeleton with scales omitted. × $\frac{4}{5}$ approx.

HORIZON AND LOCALITIES: Lower Kimmeridgian of the Eichstätt region, Bavaria, Germany.

MATERIAL. BM(NH): 37935a & b, 37099, 37088, P5547; RSM: 1893.120.5; Mü: 1964.23.145, AS.1.767; CM: 4718, 4824; Ei: four specimens.

REMARKS. Vetter's (1881) incomplete specimen of *H. parvus* most probably belongs to this species, as does his *N. macropterus*. As explained above, Woodward's specimens of this species were incorrectly ascribed to *P. speciosus*.

DESCRIPTION. (i) General features. *P. elongatus* displays the characteristic form of the genus, in which the depth of the trunk decreases posteriorly from the level of the first dorsal fin-ray to form a narrow caudal peduncle (Fig. 22). Most specimens are about 100 mm in length.

(ii) Skull roof and braincase. The skull roof is exposed in dorsal view in the acid-prepared specimen 1964.23.145 (Fig. 23). It resembles that of *Macrosemius* in its general proportions, although the preorbital region of the frontals is shorter in comparison with the postorbital region.

The parietal has similar relationships to the surrounding bones as in the type genus; in contrast, however, the frontoparietal suture is serrated. As usual, the supratemporal commissure passed through the parietal close to the posterior border; the canal was exposed dorsally by a single fenestration, and also along a short distance across the midline as it passed from one parietal to the other. Anterior to the commissure the surface of the parietal forms stout, radiating ridges bearing tubercles of ganoine. These ridges decrease in height and disappear before the suture with the frontal is reached. The anterior and middle pit-lines form short, deep grooves, lying at about 45 degrees to each other, across the ridges.

The supratemporal is not preserved; it must have been very similar in form and position to that of *Macrosemius*. The right dermopterotic is preserved in a crushed state. It resembles that of the type genus; the wide sensory canal was exposed by two or three large fenestrae.

The frontal forms a straight median suture with its fellow; its surface is devoid of ganoine and bears no ridges. The supraorbital sensory canal entered the bone through a lateral opening immediately behind the orbit. As the canal passed medially it was exposed by three fenestrae of regularly decreasing size aligned close to the posterior border of the orbital embayment of the frontal. Between the embayments the canal converged gradually with the midline; it was exposed in this region by one small and two elongated openings facing medially and giving onto the sunken surface of the frontal alongside the median suture. A bundle of extremely fine diverging tubes extends from the canal tube midway above the orbit to the surface of the bone in the anterior part of the orbital region. A number of much shorter tubes extends from the posterior part of the canal, following a curved path to the surface. Anterior to the orbit, as usual, the frontal forms an open trough which housed the supraorbital sensory canal.

The nasal is not preserved; it probably formed a scroll around the sensory canal as usual.

The rostral is visible in ventral view in 1964.23.145. It enclosed only a short length of the rostral commissure on either side of the midline. The bone forms two broad wings which lay above the anterior ends of the antorbitals.

The vomerine teeth are exposed from below in 1964.23.145 (Fig. 26). These are tall and conical,

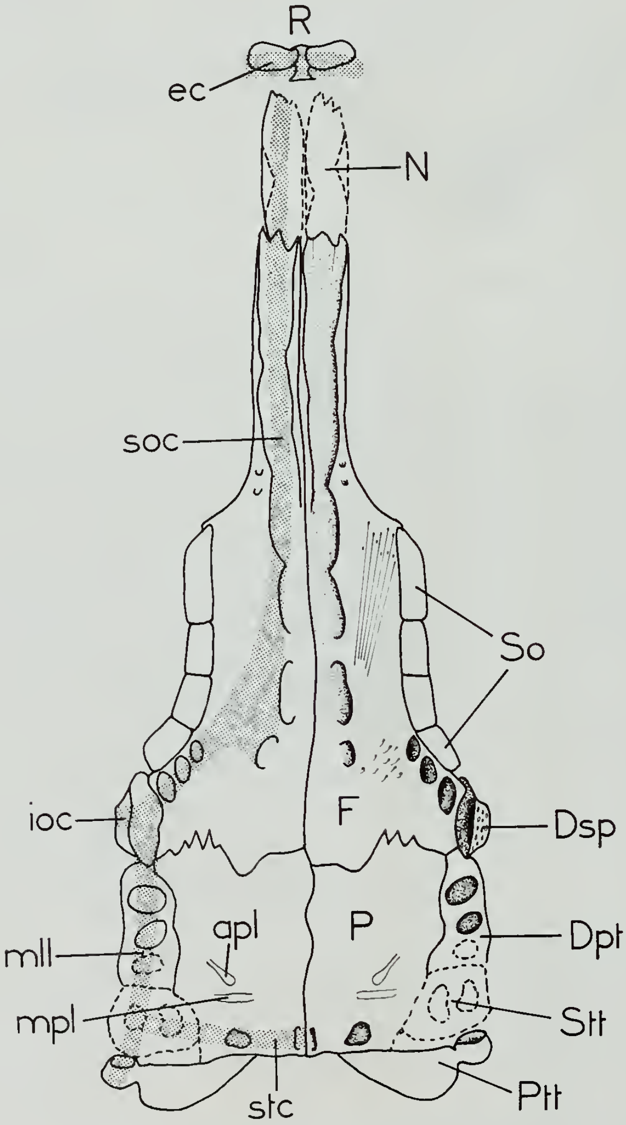

Fig. 23 *Propterus elongatus* Wagner. Skull roof, as preserved in 1964.23.145. Dashed lines indicate restored parts. × 6.

and form a single transverse row posterior to and parallel with the premaxillary tooth-row, as in the type genus. Each vomer bears about six teeth.

The parasphenoid is stout and curves downwards slightly to the snout region. Its lateral borders form a narrow suborbital shelf. A stout basipterygoid process, similar to that of *Macrosemius*, is visible in 37099.

The orbitosphenoid (Fig. 24) is a large bone reaching from the parasphenoid to the skull roof and presenting in lateral profile the form of an incomplete disc, with a deep, concave emargination in the posterodorsal quadrant. A stout flange extends laterally from the dorsolateral surface. The posterior surface of this flange is smooth, presumably for the reception of the eyeball.

(iii) Circumorbital series. Supraorbitals are present in only one of the specimens (37935b); they have been lost from, or were absent in, the others. They number four; the foremost is the longest and tapers anteriorly. The central two are rectangular and the posterior one triangular.

There are ten bones, as in all macrosemiids, in the infraorbital series. The antorbital consists of a simple tube, tapering as it turns medially towards the rostral (Figs 24, 26); the lateral wall is pierced by several large fenestrae occupying the entire width of the tube.

The first seven scroll-like infraorbitals, lying below the level of the parasphenoid, are preserved in 37935 and 1893.120.5. As in *Macrosemius*, the anterior three extend ventrally to cover the lateral surface of the maxilla; their edges in contact are straight. The following four infraorbitals extend to the level of the basipterygoid process; their arrangement and form are very similar to those of the type genus. The eighth and ninth members of the series form the usual perforated tubes around the upper part of the infraorbital canal; as in *Macrosemius*, the lower is about twice the length of the upper.

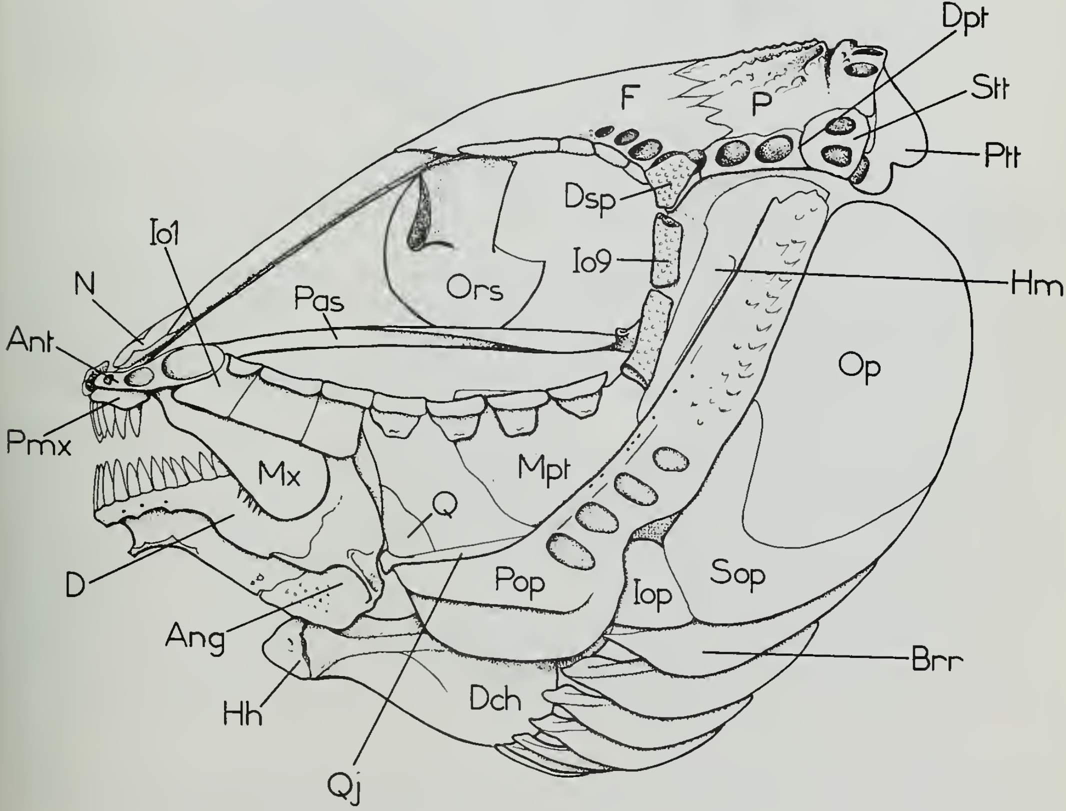

Fig. 24 *Propterus elongatus* Wagner. Restoration of skull. × 5 approx.

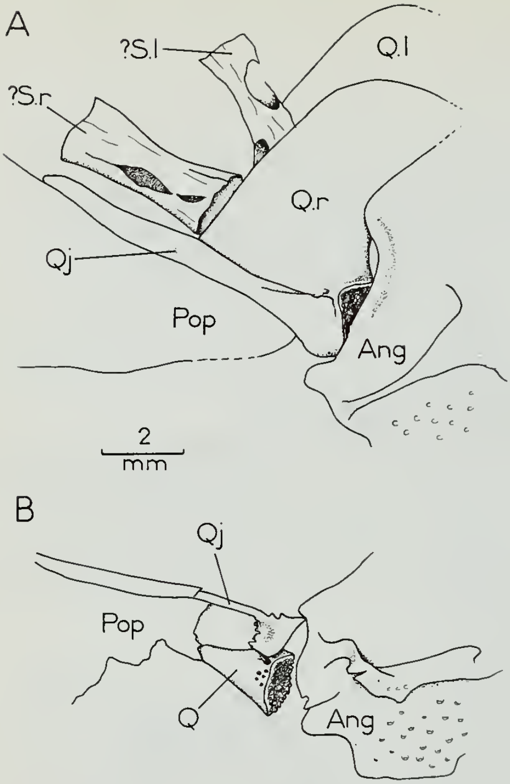

Fig. 25 *Propterus elongatus* Wagner. Lateral views of right jaw articulation, as preserved in A, 1893.120.5 and B, 1964.23.145.

The dermosphenotic is again typical of the family; it forms a short, perforate tube, with a flared dorsal end, which lies against the lateral surface of the sphenotic. Its anterior wall is not prolonged dorsally (1964.23.145).

(iv) Hyopalatine bones. None of the specimens displays the palate in its entirety. The oral border of the palate rises much more steeply from the jaw articulation than it does in *Macrosemius*. A few tall ectopterygoid teeth are visible in 1964.23.145 (Fig. 26). The metapterygoid is much as it is in the type genus; this bone contacts the quadrate only in the larger specimens. The hyomandibular is not fully exposed in the specimens, although in one of them (37099) the lateral flange may be seen.

The quadrate is exposed in 1893.120.5. Its long dorsoposterior edge is slightly convex (Fig. 25A). The quadratojugal is slender, extending for about twice the length of the quadrate against which it lies. The shaft of the bone is slightly expanded laterally midway along its length; it rests as usual upon the upper surface of the ventral arm of the preopercular. Distally the shaft expands and abuts against the lateral surface of the quadrate condyle; it is not clear from this specimen whether fusion occurs between the two bones in this region as it does in *Macrosemius*. In another (1964.23.145), however, the preopercular and quadratojugal have together been twisted through about 90 degrees, away from the quadrate. The expanded head of the quadratojugal has pulled away quite cleanly from the quadrate and the two bones evidently were not fused (Fig. 25B). This specimen also shows clearly two notches on the lateral surface of the quadratojugal head.

In specimen 1893.120.5 (Fig. 25A) there lies a short stout bone, about four times as long as broad, in the space between the metapterygoid and quadrate. The remains of a similar element are associated with the quadrate of the left side. The crushed, flattened state of these bones indicates their origin in cartilage. Although probably displaced dorsally from its position in life, this element is probably the symplectic, a bone which has not been found in any other macrosemiid specimen, perhaps due to faulty preservation. There can be little doubt, however, that if present it formed no articulation with the mandible as it does in *Amia* and the extinct halecomorph holosteans (Patterson 1973). In most other groups the symplectic extends along the medial surface of the quadrate, although in certain forms in which the jaw articulation is very forwardly placed, for example *Lepisosteus* and some teleosts such as *Chanos* (Gosline 1967 : 238, text-fig. 1), contact between symplectic and quadrate is almost or entirely lost. A tendency towards this condition appears to be exhibited by *Propterus*.

(v) Dermal upper jaw. The head of the premaxilla is broad and bears six tall, pointed teeth similar to those on the vomer. The point of each tooth is formed by a cone of enamel. The nasal process of the premaxilla is not exposed in the specimens.

The upper and lower borders of the maxilla diverge posteriorly from the medial process; the hind edge is convex. A row of very small needle-like teeth occupies the posterior half of the oral border.

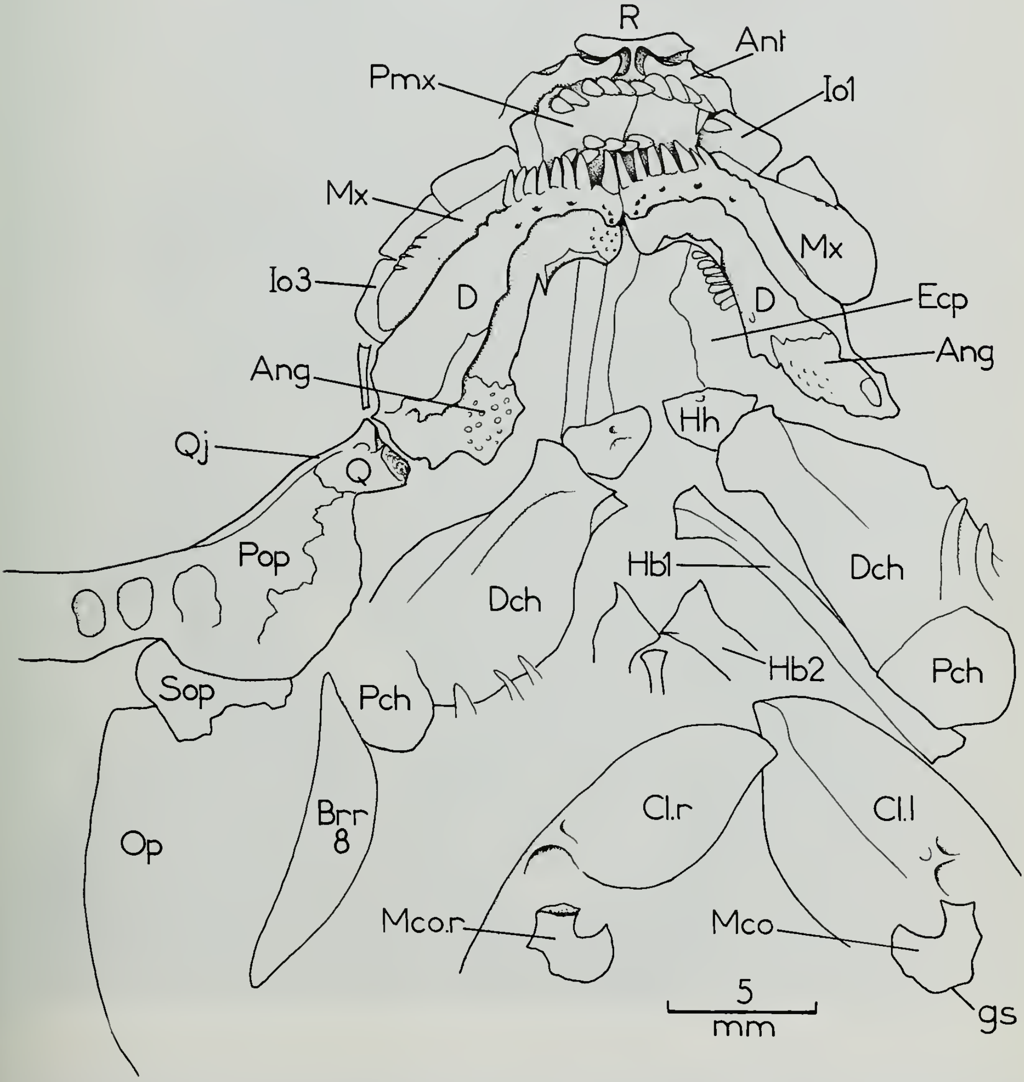

Fig. 26 *Propterus elongatus* Wagner. Dorsoventrally-crushed skull in ventral view, as preserved in 1964.23.145.

Plate 3 *Propterus elongatus* Wagner. Positive print of a radiograph of the skull and anterior part of the trunk, transfer preparation of 1893.120.5. × 3.

Plate 4 *Propterus elongatus* Wagner. Positive print of a radiograph, transfer preparation of 1893.120.5. × 1·125.

(vi) Lower jaw. Only the dentary and angular bones can be described from the specimens. The dentary bears about 11 teeth; these are tall and closely set, resembling those of the premaxilla. A series of six foramina pierce the dentary below the tooth-row. As in other macrosemiids the mandibular sensory canal lay in a very wide, open trough in the dentary. The canal continued along a trough formed by the angular; in contrast to the condition in *Macrosemius* a complete, slender arch of bone spanned the canal below the quadrate articulation. The medial wall of the trough is pierced by many small holes, and forms an interdigitating suture with the dentary. Above the canal the angular forms a long slender prolongation which passes along the upper edge of the canal as in the type genus.

(vii) Preopercular, hyoid arch and opercular series. The fore edge of the preopercular follows a regular curve from the skull roof to the jaw articulation. The lower part of the dorsal arm is pierced by large fenestrae (two in 37935b, four in 1893.120.5) which exposed the sensory canal. In the upper part of the dorsal arm the canal communicated with the exterior through many dorsally-directed pores (Fig. 24). As in other members of the family, the lower surface of the canal was exposed along the entire length of the ventral arm of the preopercular.

The opercular is narrow, about twice as deep as wide. The outer surface of the bone is slightly wrinkled and bears small, pointed, isolated tubercles of ganoine (1964.23.145). The subopercular forms the usual vertical process along the leading edge of the opercular; its surface is smooth and devoid of ganoine. The interopercular is, as in other macrosemiids, small and remote from the mandible. There are seven or eight branchiostegal rays; the upper rays are acinaciform. Their blades are deeper than those of *Macrosemius*. The condition of the uppermost ray cannot be determined from the specimens.

The ceratohyals are exposed in 1964.23.145. Both proximal and distal ossifications are closely similar to those of the type genus. The single hypohyal is also visible in this specimen. It consists mainly of cancellous endochondral bone bounded on its ventromedial surface by perichondral bone in the form of a laterally-buckled disc (Fig. 26); the centre of the disc is pitted, presumably at the point of insertion of the tendon of the sternohyoideus muscle.

(viii) Branchial arches. The elongated slender first hypobranchial is exposed in 1964.23.145. The anterior ends of the stouter second hypobranchials are also visible.

(ix) Vertebral column. There are about 40 vertebral segments between the skull and the base of the axial lobe. The column is not exposed in any of the specimens, but information about its structure can be obtained from a radiograph of the acid-prepared specimen 1893.120.5 (Pl. 4). Six median supraneurals occur behind the skull; the anterior four lie in front of the dorsal fin, and the remaining two interdigitate between the second and third and between the third and fourth proximal dorsal radials respectively. The first six vertebral segments appear to form dorsal crescentic hemicentra only; the remainder of the axis forms no centra. The same radiograph reveals that the neural spines are paired throughout the first 29 segments at least. There are about 20 pairs of abdominal ribs.

(x) Pectoral girdle and fin. The post-temporal forms a triangular lamina which articulated in a groove along the posterior edge of the parietal. The lateral part of the bone is not preserved; it probably formed an inflated tube around the cephalic division of the main lateral line as in other macrosemiids.

The cleithrum is exposed in lateral view in 37935b (Fig. 27). The anteromedial edge of the ventral arm forms two shallow embayments; the posteroventral edge is gently convex. A single row of denticles, each bearing a single cusp, is aligned vertically along the lateral face of the dorsal arm. The dorsolateral surface of the ventral arm forms a rounded zone for the lower part of the opercular membrane, as is usual. The lower surface of this rounded region is exposed in 1964.23.145 (Fig. 26); it is defined medially by a ridge which presumably also marked the limit of the insertion of the ventral trunk musculature. Immediately posterior to the ridge occurs a deep recess for the reception of the endoskeletal pectoral girdle.

The ossified part of the scapulocoracoid forms a simple stout arch of bone (Fig. 26). One foot of the arch forms a broad surface which fitted into the recess on the cleithrum; the other foot presumably continued as an anterior cartilaginous process which in life made contact with the ventral surface of the cleithrum, as in *Lepisosteus* (Jessen 1972: text-fig. 4). The glenoid surface for the articulation of the proximal radials of the fin occurs on the outer part of the arch.

The endoskeleton of the fin is not clearly preserved; there appear to be five proximal radials increasing in length posteriorly. There are about 15 pectoral fin-rays. The leading ray, devoid of basal and fringing fulcra, consists of two fused hemitrichia terminating below the segmented part of the succeeding ray (Fig. 28B). The leading ray is not as reduced as that of *Macrosemius rostratus*, however, and shows signs of incomplete fusion between the two hemitrichia; it bears dorsally- and ventrally-directed processes at its base, as do the remaining rays, which are segmented and branch distally.

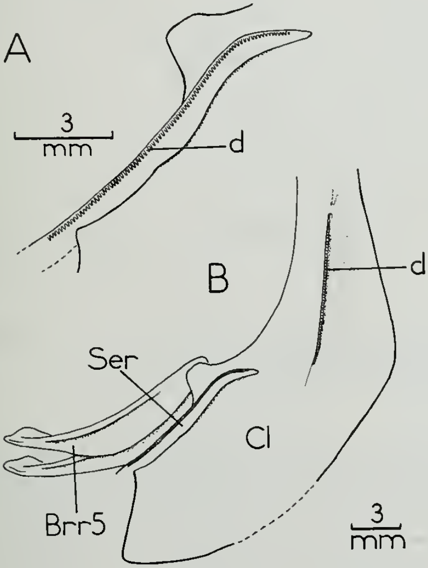

Fig. 27 *Propterus elongatus* Wagner. Part of pectoral girdle, as preserved in 37935b. A, left serrated appendage. B, part of left cleithrum, serrated appendage and two branchiostegals.

A slender serrated appendage is preserved in 37935 lying along the upper margin of the ventral arm of the cleithrum. The distal end of the bone tapers and turns posteriorly; it appears to have projected into the opercular cavity. A single row of denticles, similar to those of the cleithrum, extends along the lateral surface close to the leading edge (Fig. 27). The homologies of the serrated appendage are discussed below (pp. 216–7).

(xi) Pelvic fin. This consists of six rays. The leading ray is preceded by four stout basal fulcra and a thick saddle-shaped scale devoid of denticles (Fig. 28A). The first two basal fulcra are unpaired and short, with broad bases. The third is twice the length of the second and is also unpaired, although cleft almost to the tip. The last basal fulcrum is paired and succeeded by fringing fulcra. All the rays are jointed and bifurcate twice. The hemitrichia form anterolaterally-directed flanges at their bases which overlap the preceding ray, thus forming a very compact fin base.

(xii) Dorsal and anal fins. The dorsal fin is divided; it extends from the dorsal angulation of the body to the caudal peduncle. In this species both the anterior and posterior parts of the fin are tall, with a convex outline. The two parts are very close together; there are between 14 and 16 fin-rays in each. The anterior dorsal is preceded by about seven slender basal fulcra. The leading ray is unpaired and unsegmented and extends slightly beyond the basal segment of the second ray. The first three radials consist of the proximal ossification and presumably the distal cartilaginous part alone; the middle segment is absent. The remainder of the fin-rays articulated with tripartite radials as usual. The posterior lobe of the dorsal fin, arising above the 20th vertebral segment, is completely devoid of fulcra and follows closely behind the anterior dorsal. The discontinuity in the fin is reflected in the inclination of the proximal radials; the proximal radial of the last anterior fin-ray is shorter than the others, and those of the posterior fin are inclined slightly backwards.

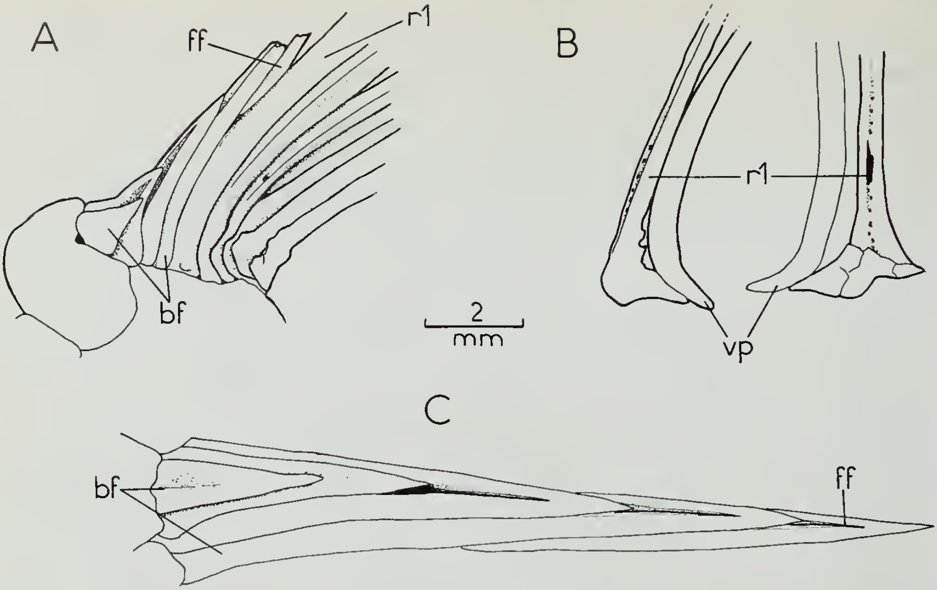

Fig. 28 *Propterus elongatus* Wagner. Bases of leading edges of various fins, as preserved in 1964.23.145. A, left pelvic fin. B, left and right pectoral fins. C, anal fin.

The anal fin was supported by six rays; it arises below the level of the 28th vertebral segment. Four unpaired basal fulcra extend along the proximal half of the leading edge of the fin. The third and fourth basal fulcra are cleft to within a very short distance of the pointed tip (Fig. 28C). The first fringing fulcrum is unpaired but again deeply cleft. The remainder of the fringing fulcra extending along most of the length of the leading ray are paired. The base of the anal fin is short and compact, in contrast to the condition in *Macrosemius*, and the first ray extends beneath the caudal fin. The remaining rays become progressively shorter, to form the slightly convex profile of the hind border of the fin.

(xiii) The caudal fin is deeply forked, with seven rays emanating from the axial lobe and eight, as usual, arising below this (Fig. 29B). The upper basal fulcra are deeply divided and extended basally, forming two tapering prongs which straddled and articulated with the epurals (Fig. 29A). The lateral borders of these fulcra taper posteriorly from the level of the cleft and then run parallel for a short distance before converging to a sharp point. The series continues along the uppermost fin-ray with about 13 fringing fulcra, of which the first eight (in 37099) are unpaired.

The uppermost fin-ray forms a continuation of the longest axial lobe scale-row and is not inserted below the squamation, as in the type genus. The following five rays form thin, closely-grouped rods proximally which penetrate beneath the axial lobe squamation and clasp the upper hypurals. The basal part of the lowermost axial lobe ray clasps the tip of its hypural and is separated from the upper rays, although its distance from the succeeding rays is greater. The ventral border of the caudal fin bears basal and fringing fulcra. The axial lobe squamation is described below.

(xiv) The scale-rows correspond to the segmentation; there are about 37 scales along the main lateral line and about 15 in the deepest transverse row. Most of the abdominal scales are deeper than wide, with the posterior edge denticulated and slightly convex; all the scales are thin. The most extensive ganoine covering on the scales occurs in the posterior half of the body, as in *Macrosemius*; anteriorly the ganoine is restricted to the hind region and to the denticles. The postcleithral scales are nowhere clearly exposed.

The ventral surface of the body between the pelvic and anal fins is visible in 1964.23.145; the scales in this region are roughly square. Denticles are present only on the median scales where they are few and large. There is a very large preanal scale and two lateral anal scales (Fig. 29). In contrast to those of the type genus, all three bear stout denticles and ganoine ridges.

The axial lobe squamation is not well preserved in any of the specimens, although it can be reconstructed from 1893.120.5. The lobe is larger in comparison with the remainder of the caudal area (Fig. 30) than it is in *Macrosemius*. There are about seven rows with the usual orientation. The scales are thick and bear dorsally-inclined serrations along their posterodorsal edges. The lateral line ends below the axial lobe.

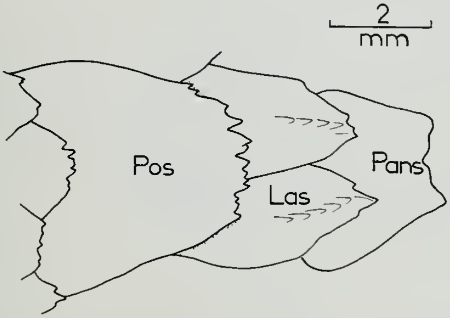

Fig. 29 *Propterus elongatus* Wagner. Circumanal scales, as preserved in 1964.23.145.

Propterus microstomus Agassiz 1834

Fig. 31

1834 *Propterus microstomus* Agassiz : 386.
1835 *Notagogus zieteni* Agassiz, **2** : pl. 49, fig. 1.
1839 *Propterus microstomus* Agassiz, **2** : pl. 50, figs 5, 6.
1844 *Notagogus zieteni* Agassiz, **2**, 1 : 10, 293.
1844 *Propterus microstomus* Agassiz, **2**, 1 : 296.
1851 *Propterus microstomus* Agassiz; Wagner : 66.
1851 *Notagogus zieteni* Agassiz; Wagner : 65.
1851 *Propterus gracilis* Wagner : 68.
1851 *Propterus speciosus* Wagner : 67; pl. 4, fig. 1.
1863 *Propterus microstomus* Agassiz; Wagner : 645.
1895 *Propterus microstomus* Agassiz; Woodward : 183.
1914a *Propterus microstomus* Agassiz; Eastman : 407; pl. 63, fig. 1.
1914a *Propterus conidens* Eastman : 407; pl. 62, fig. 2.
1949 *Propterus microstomus* Agassiz; Vianna : 13; pl. 1.
1966 *Propterus microstomus* Agassiz; Schultze : 275, text-figs 7, 31, 32; pl. 49, fig. 2.

DIAGNOSIS. *Propterus* reaching standard length of 150 mm, although most specimens are about half this size; mean proportions as percentage of standard length: head length 33%, trunk depth 38%, predorsal length 40%, prepelvic length 60%, preanal length 84%; fin-ray counts: D(ant.) 10–13, D(post.) 10–14, P 17, V 6, A 5, C 15; about 36 lateral line scales; scales thin; two lobes of dorsal fin separated by a gap; anterior dorsal fin outline concave; no fulcra on posterior dorsal fin; caudal fin-rays bifurcating a maximum of twice.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.7.268. From the Lower Kimmeridgian of Kelheim, Bavaria.

HORIZONS AND LOCALITIES. Lower Kimmeridgian of Eichstätt and Kelheim regions of Bavaria; Lusitanian of Cabo Mondego, Portugal.

MATERIAL. Mü: AS.7.268, AS.5.30, AS.1.634, AS.1.766, 1964.23.143, 1964.23.146; CM: 4468, 4825; Ei: five specimens.

REMARKS. As discussed above, the type specimen of Wagner's (1851) *P. speciosus* belongs to this species; so too does Eastman's (1914a) *P. conidens*. Details of the skull of *P. microstomus* remain

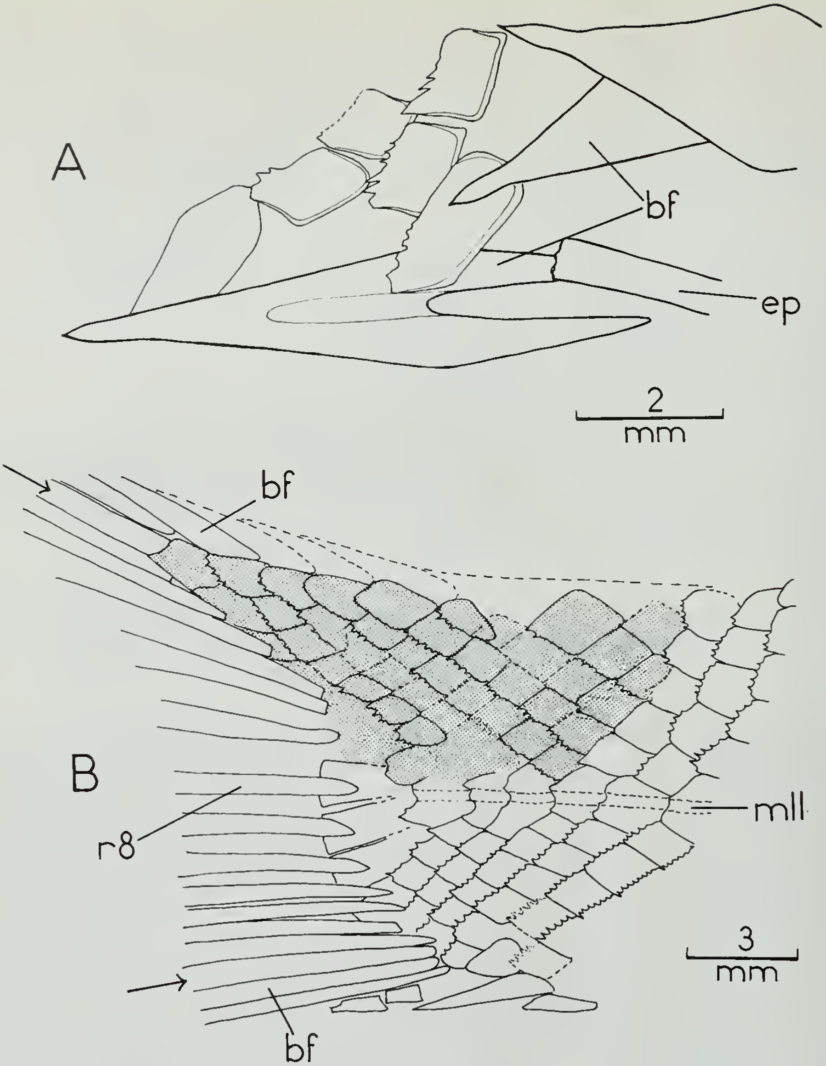

Fig. 30 *Propterus elongatus* Wagner. A, scattered dorsal basal fulcra of caudal fin, as preserved in 1964.23.145. B, caudal fin squamation restored from 1893.120.5, axial lobe shaded.

poorly known, since no specimens were available for preparation in acetic acid. However, this fish closely resembles *P. elongatus* in its form, proportions and squamation, and the available evidence indicates that their skulls were very similar as well.

Description. (i) General features. *P. microstomus* rarely exceeds 75 mm in standard length. It is the only member of the genus having an emarginated anterior dorsal fin (Fig. 31).

(ii) Dorsal fin. In contrast to the condition in *P. elongatus*, in which the two parts of the dorsal fin stand close together, these are separated by a distance equivalent to the width of four scales in *P. microstomus*. The leading ray exceeds the depth of the trunk in length; it is preceded by about seven basal fulcra and bears two elongated fringing fulcra. The 12 or so remaining rays of the anterior dorsal decrease rapidly in height, forming a deeply concave outline. The posterior dorsal fin, also comprising about 12 rays, is low and convex in outline.

(iii) Squamation. The number of rows and the pattern of the scales closely resemble those of *P. elongatus*. The ventral and circumanal scales have been drawn and described by Schultze

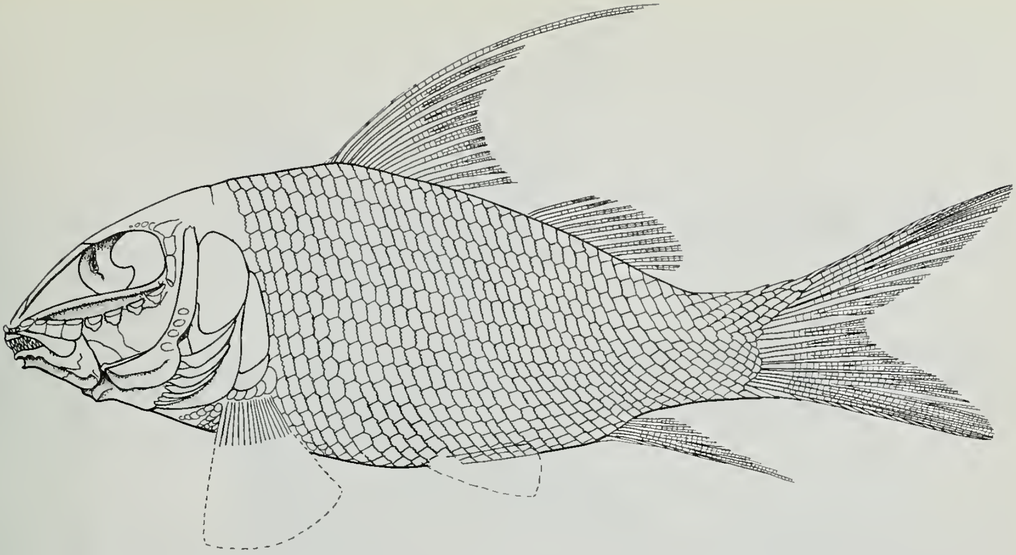

Fig. 31 *Propterus microstomus* Agassiz. Restoration of skeleton. $\times \frac{3}{5}$ approx.

(1966 : 275, text-figs 7, 31; pl. 49, fig. 2). The ventral squamation is preserved in AS.1.634 and consists of about 20 rows at right angles to the main transverse rows; such an arrangement occurs in other groups, for example the chondrostean Haplolepidae (Westoll 1944 : text-figs 1, 13) and may be common to most actinopterygians with rhomboid scales. These scales tend toward a cycloid structure; they are rounded, lack ganoine and pegs-and-sockets, and bear both concentric and radial markings.

Propterus scacchi (Costa 1850)

1850 *Rhynchoncodes scacchi* Costa : 317; pl. 5, fig. 5.
1864 *Rhynchoncodes macrocephalus* Costa : 102; pl. 9, figs 10, 11.
1895 *Propterus scacchii* (Costa) Woodward : 185; pl. 3, fig. 6.
1912 *Propterus scacchi* (Costa); Bassani & d'Erasmo : 213; pl. 4, fig. 3.
1914 *Propterus scacchi* (Costa); d'Erasmo : 80; pl. 9, fig. 5.

DIAGNOSIS. *Propterus* reaching standard length of 60 mm; mean proportions as percentage of standard length: head length 37%, trunk depth 35%, predorsal length 48%, prepelvic length 65%, preanal length 88%; fin-ray counts: D(ant.) 10–11, D(post.) 10–11, A 6, C 14; outline of anterior dorsal fin convex; no fringing fulcra on posterior dorsal fin; caudal fin-rays branch a minimum of twice.

HOLOTYPE. Specimen in Universita di Napoli, Istituto di Paleontologia.

HORIZON AND LOCALITY. Lower Cretaceous (?Albian or Aptian) of Torre d'Orlando, near Castellamare, Naples, Italy.

MATERIAL. BM(NH): P3613.

REMARKS. Only Woodward's specimen was available for examination; little can be added to the early accounts by Italian workers.

Propterus vidali Sauvage 1903

1903 *Propterus vidali* Sauvage : 9; pl. 2, fig. 1.
1956 *Propterus vidali* Sauvage; Bataller : 114; pl. 14, fig. 1.

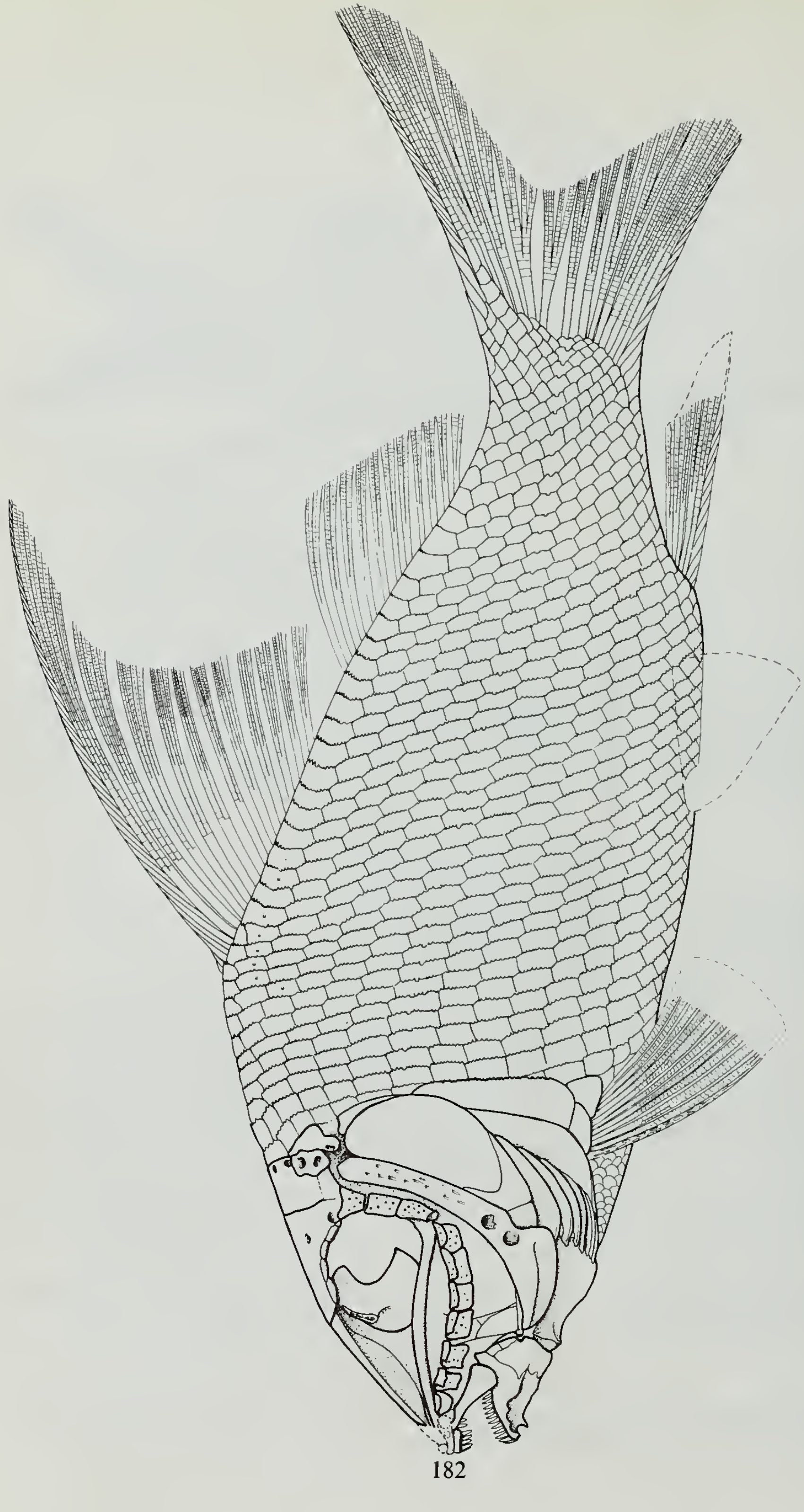

Fig. 32 *Histionotus oberndorferi* Wagner. Restoration of skeleton. Skull roof and infraorbitals restored from *H. angularis* Egerton. × $\frac{4}{5}$ approx.

DIAGNOSIS. *Propterus* reaching standard length of 130 mm; proportions as percentage of standard length: head length 27%, trunk depth 35%, predorsal length 43%, prepelvic length 50%, preanal length 75%; fin-ray counts: D(ant.) 10–11, D(post.) 10–11, C 14–15; about 35 lateral line scales; scales thick; outline of anterior dorsal fin slightly convex; fringing fulcra on posterior dorsal fin; caudal fin-rays bifurcate a maximum of six times.

HOLOTYPE. Specimen in Museo Municipal de Geologia, Barcelona.

HORIZON AND LOCALITY. Neocomian of Santa-Maria-de-Meya, Lerida, Spain (these beds have traditionally been treated as Kimmeridgian in age, like the classic localities of Germany and France, but recent micropalaeontological work (Brenner, Geldmacher & Schroeder 1974) shows them to be Neocomian, probably Valanginian).

MATERIAL. BM(NH): P10993, P10994.

REMARKS. This species is at present being studied by Mlle S. Wenz. The above provisional diagnosis, based upon the BM(NH) specimens, is given for comparison. The species is remarkable for the presence of fringing fulcra on the posterior dorsal fin, thick scales with very small pectinations and highly branched caudal fin-rays.

Genus *HISTIONOTUS* Egerton 1854

DIAGNOSIS. Medium to large, deep-bodied macrosemiid fishes; dorsal profile of trunk bent at first dorsal fin-ray; ganoine present on frontals and parietals, frontoparietal suture straight; supraorbitals large; gape very small, the jaw articulation lying anterior to the orbit; dentigerous expansion of maxilla pierced by small foramen, upper and lower borders concave, posterior edge convex, teeth absent or greatly reduced; dentary with closely-set styliform teeth; anterior edge of preopercular forming a smooth curve, sensory canal with many pores in dorsal arm; opercular, subopercular, interopercular and uppermost branchiostegal ray with radiating ridges of ganoine; leading ray of pectoral fin bearing long ridges of ganoine, probably fused fringing fulcra; base of anal fin compact, leading ray extending below caudal fin and bearing fringing fulcra; caudal fin deeply forked; dorsal fin divided, extending from dorsal angulation to the caudal peduncle, rays bifurcating profusely, leading ray bearing deeply overlapping fringing fulcra and greatly elongated, remaining rays of anterior dorsal decreasing rapidly in height to form a concave upper profile; posterior dorsal fin low, convex; vertebral centra forming thick cylinders; squamation forming pattern of deepened hexagons on trunk, scales adjoining dorsal fin each extended posteriorly along their dorsal edges and bearing pits of dorsal lateral line; postcleithral scales large, bearing ganoine ridges.

TYPE SPECIES. *Histionotus angularis* Egerton 1854.

INTRODUCTION. The genus *Histionotus* was erected by Egerton (1854) to contain one species, *H. angularis* from the Purbeck of southern England. Wagner (1863) described another species, *H. oberndorferi*, from the Lower Kimmeridgian of Bavaria, and Vetter (1881) added *H. parvus* from the same locality. Previously Thiollière (1873) had given a brief description of another species from the Lower Kimmeridgian of Cerin (Ain, France), *H. falsani*, of which Saint-Seine (1949) gave a fuller account. Finally, Eastman (1914a) added *H. reclinis* to the genus.

REMARKS. Vetter's (1881) imperfect specimen belongs to *Propterus elongatus* Wagner, and *H. reclinis* Eastman is an example of *Furo latimanus* Agassiz.

Histionotus angularis Egerton 1854

Figs 33–34

1854 *Histionotus angularis* Egerton : 434.
1855 *Histionotus angularis* Egerton; Egerton : 2; pl. 5.
1889 *Histionotus angularis* Egerton; Mansell-Pleydell : 241; pl. 7.
1895 *Histionotus angularis* Egerton; Woodward : 174.
1918 *Histionotus angularis* Egerton; Woodward : 77; pl. 17, figs 1–5.
1966 *Histionotus angularis* Egerton; Schultze : 306, text-fig. 48a.

Diagnosis. *Histionotus* reaching standard length of 150 mm; mean proportions as percentage of standard length: head length 30%, trunk depth 40%, predorsal length 37%, prepelvic length 53%, preanal length 77%; dentary teeth tall and styliform; the two lobes of the dorsal fin close together, with a total of *c.* 25 rays.

Holotype. British Museum (Natural History), P577.

Horizon and Localities. Purbeck Beds of Dorsetshire and Wiltshire, England.

Material. BM(NH): 46421, P577, P3614, P5935.

Remarks. Woodward (1918 : 77; pl. 17, figs 1–5) has given a detailed account of this species. The material is redescribed below, however, in the light of knowledge gained from other macrosemiid genera.

Description. (i) General features. *Histionotus angularis* is a deep-bodied, laterally-compressed fish; its average proportions are given in the diagnosis above.

(ii) Skull roof and braincase. The skull roof is displayed in P5935 and P577 (Fig. 33). The parietal is large and approximately rectangular, forming straight sutures with its fellow, the frontal, and the dermopterotic. The parietal contacts the supratemporal along an identation in its posterolateral corner. The supratemporal commissure crossed close to the posterior edge of the bone and was exposed dorsally by a small fenestration, as in *Propterus.* The canal emerged from its tube medially and crossed the midline unenclosed. Anterior to and parallel with the supratemporal commissure lies a short groove which housed the middle pit-line; no other pit-lines are visible. Thick ganoine rugae radiate from this region.

The supratemporal is, as usual, small, and does not reach the midline of the skull. Its irregular form is difficult to interpret in the specimens. It appears to have formed a wide thin-walled tube around the cephalic division of the main lateral line, together with a medial portion through

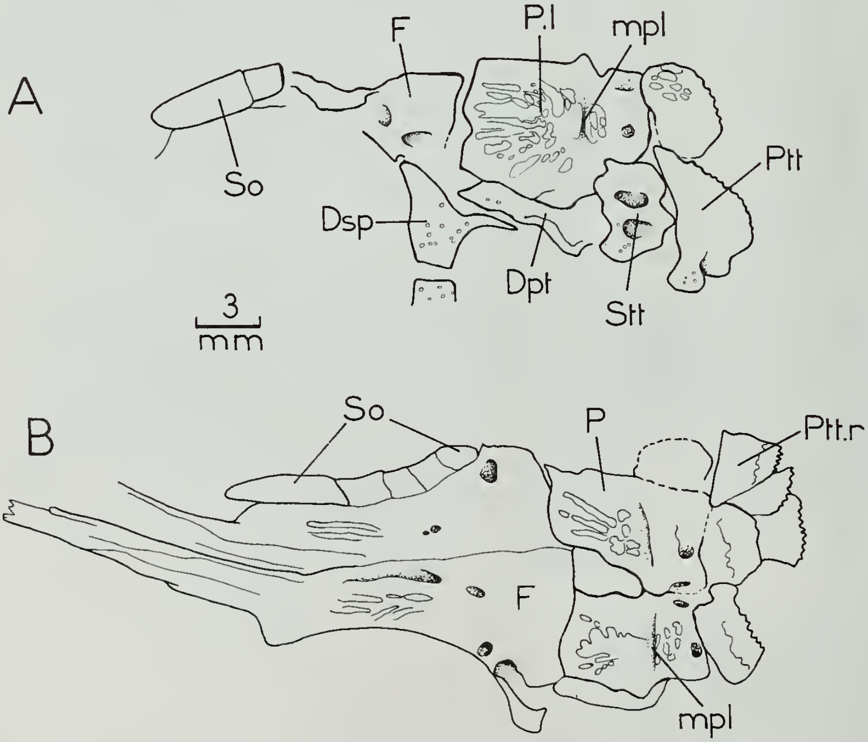

Fig. 33 *Histionotus angularis* Egerton. Skull roof, as preserved in A, P577 and B, P5935.

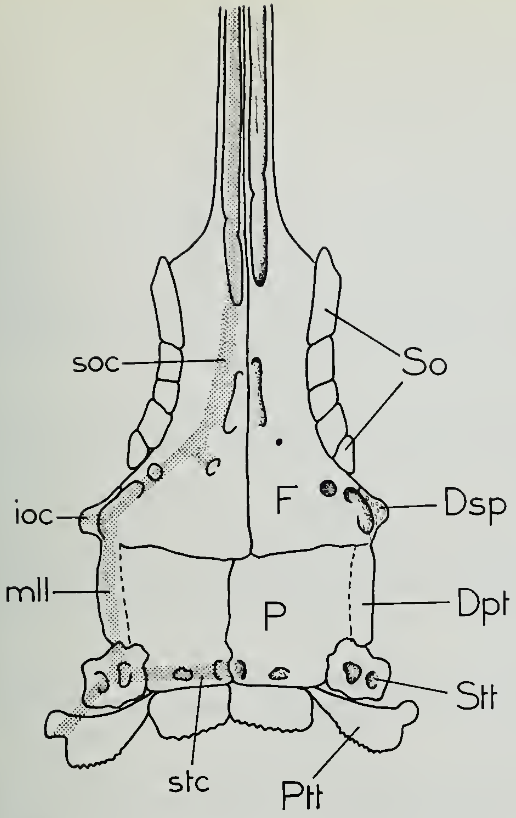

Fig. 34 *Histionotus angularis* Egerton. Restoration of skull roof. The probable medial limit of the dermopterotic is indicated by dashed lines; the nasals are omitted. ×4½ approx.

which passed the lateral part of the supratemporal commissure, where it was exposed by a large fenestration. The main lateral line continued anteriorly through the dermopterotic; the form of this bone is obscured by crushing in the specimens.

The short postorbital region of the frontal is wide, as usual. The supraorbital sensory canal entered the frontal laterally, behind the orbit, and passed medially; the canal in the supraorbital region is exposed by one or two elongated openings (Fig. 34), much as in *Propterus*. In the preorbital region the frontals form an open trough for the sensory canal as in they do all macrosemiids. They also form two lateral, vertical extensions on either side of the preorbital region of the skull; the frontals are similarly formed in *Notagogus*. Ganoine is restricted to two regions of the frontal. The smaller patch occurs close to the posterior border, while elongated rugae cover the surface between the orbital embayment and the sensory canal (Woodward 1918 : pl. 17, fig. 3).

The nasals are not preserved in the specimens. The orbitosphenoid is better known in *H. oberndorferi* described below; the remainder of the braincase remains unknown.

(iii) Circumorbital bones. There are five large supraorbitals, of which the foremost is the longest and tapers anteriorly. The remaining four are approximately rectangular; all bear a complex pattern of ridges on their surfaces.

The remains of the nine infraorbitals are discernible in P577; Woodward did not recognize them. The antorbital is crushed, but appears to have formed the usual tapering tube. The infraorbitals display the typical macrosemiid configuration; the first seven below the eye are curled over the infraorbital sensory canal, and the two behind the orbit form complete tubes.

The dermosphenotic, visible in P577, resembles that of *Macrosemius*. It forms a short, dorsally flared, vertical tube around the infraorbital sensory canal below its junction with the supraorbital canal. The anterior surface of the bone is prolonged into a stout process which abuts against the lateral margin of the frontal. Thus the dermosphenotic of *Histionotus*, while retaining the character of a member of the infraorbital series, was apparently firmly attached to the skull roof, as in *Macrosemius*.

(iv) Hyopalatine bones. A short portion of the ectopterygoid is present in 46421 and has been drawn by Woodward (1918 : pl. 17, fig. 4). The oral border bears about ten teeth; these are short and stout anteriorly, the posterior members of the row increasing in height.

When the animal is horizontal the quadrate articulation lies beneath the anterior border of the orbit, but if the skull is held with the parasphenoid horizontal, the articulation lies well in advance of the orbit. This follows because, owing to the deep trunk, the parasphenoid slopes ventrally from occiput to snout. Thus *Histionotus* has the smallest gape among macrosemiids. Although the quadrate and the remaining bones of the palate are poorly preserved, the quadratojugal is visible in P3614, and forms a long spine which lies along the upper edge of the preopercular as usual. It thickens anteriorly to form a stout rod behind the articular condyle of the quadrate. It is not clear whether the quadratojugal was fused to the quadrate at this point; in *H. oberndorferi* it is not fused.

(v) Dermal upper jaw. The premaxilla is partially preserved in 46421. The nasal process is much broader and stouter than in *Macrosemius* and appears to have extended beneath the frontals. The premaxillary teeth are slender and pointed.

The maxilla has a complex form, similar to that of *H. oberndorferi* (Fig. 35). The dorsal edge forms two shallow, smooth embayments; the oral border is concave and the hind edge convex. The maxilla appears to be toothless, although in some specimens (P577 for example) a few small pits are present along the posterior part of the oral border which may have held teeth. If present these must have been very small. A small foramen pierces the maxillary expansion in the anterior region.

(vi) Lower jaw. The mandible is badly crushed in the specimens; its component bones are more surely known in *H. oberndorferi*. The dentary teeth are styliform and very closely set. The facet for the quadrate condyle is very broad, deep and faces posteriorly.

(vii) Preopercular and opercular series. These are preserved in P577. The leading edge of the preopercular forms a regular curve from the skull roof to the jaw articulation; the greatest curvature occurs beneath the orbit. The trailing edge runs approximately parallel with the anterior border along the dorsal arm and forms an indentation at its base before continuing forward. The preopercular sensory canal communicated with the exterior through many narrow, dorsally-directed pores in the upper part of the bone, as in *Propterus*. Below this region, as usual, the canal was exposed by two or three large fenestrae and by a long ventral opening in the lower arm.

The opercular is about twice as deep as wide; its surface is completely covered by ganoine raised into a pattern of radiating ridges. The subopercular is wide and forms an ascending process along about half of the leading edge of the opercular. The dorsal border of the subopercular is deeply indented by the overlapping opercular. The surface of the subopercular is ornamented with ridges of ganoine. The interopercular is not fully exposed in the specimens; its form and size seem similar to those of other macrosemiid genera.

The uppermost two branchiostegals are visible on P577. The uppermost forms a broad blade extending along the entire ventral edges of the interopercular and subopercular. Unlike the condition of other members of the family, this ray, and to a lesser extent its predecessor, bears ganoine ridges.

(viii) Vertebral column. Several abdominal vertebrae are partially exposed in P3614. They form thick perichordal cylinders to which the neural and haemal arches are fused.

(ix) Pectoral girdle and fin. The post-temporals are preserved in P577. They resemble those of *Macrosemius* and *Propterus* in forming a broad triangular lamina medially and a short wide tube laterally around the lateral line. A few small patches of ganoine occur along the denticulated hind border (Fig. 33). The post-temporals are separated from each other by two large rectangular scales: these reduce the area of contact between the post-temporals and parietals. The surface of the two scales bears thick rugae of ganoine like those of the skull roof, unlike the even covering of ganoine on the trunk scales.

Part of the supracleithrum is visible in some specimens, but is poorly preserved. The upper part of the trailing edge is denticulated and bears ganoine. A large sensory pit is present, as in *Macrosemius.* The cleithrum is not exposed in the specimens.

The pectoral fin comprised at least ten rays. The leading ray is visible in P577; it is paired, each hemitrich bearing a row of sharply raised, elongated protuberances covered with ganoine. These are probably fringing fulcra which have fused to the ray. The postcleithral scales are described below, with the squamation.

(x) Pelvic fin. This consists of five rays, which are preceded by three large unpaired basal fulcra. Unlike in *Macrosemius* or *Propterus* the leading ray bears a series of very stout, closely-set fringing fulcra.

(xi) Dorsal and anal fins. The anal fin is not preserved; a few large fringing fulcra belonging to the fin are visible in P577. The anal fin of *H. oberndorferi* is better known.

Woodward (1918 : 79) estimated that the dorsal fin comprised about 25 rays which supported an uninterrupted fin-web. In *H. oberndorferi*, however, the dorsal fin is certainly divided. Woodward's drawing of Mansell-Pleydell's (1889) specimen of *H. angularis* suggests that the posterior 10 rays of the fin are longer than the first 15. This agrees with the condition in *H. oberndorferi*, in which the rays of the posterior lobe are longer than the last rays of the anterior lobe. In contrast with the latter species, however, all the dorsal rays are approximately equidistant from each other, so that there can have been no significant gap between the two lobes (if, as is assumed here, two lobes were present). The leading dorsal fin-ray is preceded by seven stout basal fulcra, and bears a series of large, deeply-overlapping fringing fulcra. The leading ray, not preserved distally in the specimens, was probably very long as in other species. The dorsal fin-rays all bear ganoine ridges on their lateral surfaces; this feature is not found in other macrosemiid genera.

(xii) Caudal fin. The caudal fin is deeply forked, with eight axial lobe rays and the usual eight rays below these. Paired fringing fulcra occur on the upper and lower edges of the fin. The axial lobe squamation is described below.

(xiii) Squamation. The three postcleithral scales are preserved in P577. The upper scale is very deep and extends along the greater part of the dorsal arm of the cleithrum; the lower two are much shorter. Both bear a complete layer of ganoine forming ridges similar to those on the opercular, and have smooth hind borders.

The trunk scales are deeper than broad; their posterior edges are slightly convex and bear denticulations (Woodward 1918 : pl. 17, fig. 5a). There are about 40 main lateral line scales and about 12 in the transverse row above the pelvic fins. The ganoine layer is smooth, forming slight ridges near the trailing edge which coincide with the denticulations. The scales in the ventral region between the paired fins are small and rounded; those between the pectoral fins bear tubercles and ridges of ganoine.

The lateral trunk scales form a narrow ridge on the inner surface as usual; the peg-and-socket is in alignment with the ridge (Woodward 1918 : pl. 17, fig. 5). Woodward (1918 : 79) reports that the main lateral line canal lay in a groove on the inner surface of the scale, although the canal was probably enclosed by a thin lateral wall as in *Macrosemius.* Approximately one-third of the main lateral line scales bear a small pit of the accessory lateral line. Similar pits, of the dorsal lateral line, occur on the scales alongside the dorsal fin. This region of the squamation displays several unusual features which are also found in *H. oberndorferi* and are described below.

The axial lobe of the caudal fin is covered by about seven rows of scales of which the lowermost continues into the uppermost fin-ray as usual.

Histionotus oberndorferi Wagner 1863

Figs 32, 35, 36

1863 *Histionotus oberndorferi* Wagner : 650; pl. 3.
1887 *Histionotus oberndorferi* Wagner; Zittel : 218, text-fig. 231.
1895 *Histionotus oberndorferi* Wagner; Woodward : 175.
1966 *Histionotus oberndorferi* Wagner; Schultze : 258, text-fig. 15.

DIAGNOSIS. *Histionotus* reaching 200 mm standard length; mean proportions as percentage of standard length: head length 31%, trunk depth 40%, predorsal length 40%, prepelvic length 57%, preanal length 78%; dentary teeth stout, conical; dorsal fin lobes separated by a gap, and with a total of about 22 rays.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.19.1.

HORIZON AND LOCALITY. Lower Kimmeridgian of the Kelheim region, Bavaria, Germany.

MATERIAL. Mü: AS.19.1, 1887.5.22.

REMARKS. The proportions of the body of this species are almost identical to those of the type species, from which it differs in the shape of the dentary teeth. *H. oberndorferi* is extremely rare; the above two specimens are the only examples known, and further knowledge of the skull may eventually help to separate the two species more definitely. *Histionotus* has hitherto been thought to possess a single dorsal fin, but specimen 1887.5.22 shows clearly that it is divided.

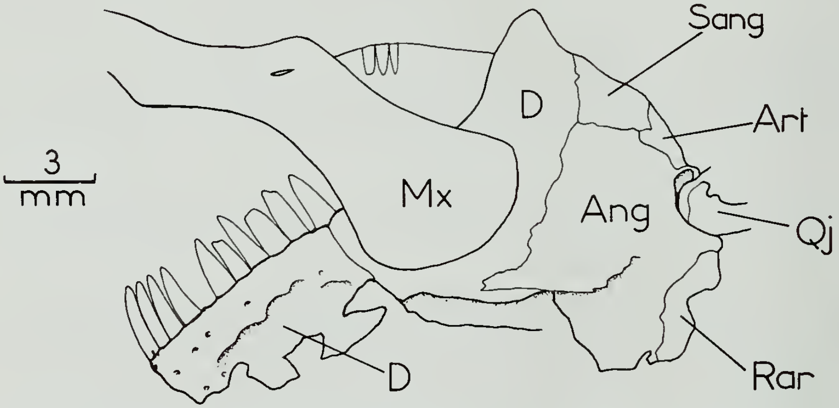

Fig. 35 *Histionotus oberndorferi* Wagner. Upper and lower jaws, as preserved in AS.19.1.

DESCRIPTION. (i) Skull. Details of the skull roof, preopercular, opercular and infraorbital series remain unknown. Fig. 36 was drawn from the impression of the skull in 1887.5.22, with details added from *H. angularis*.

The orbitosphenoid is preserved in AS.19.1 and in impression in 1887.5.22. This bone is very similar to that in *Propterus*; its hind margin is deeply emarginated, and it forms a large anterior lateral flange against which the eyeball presumably rotated.

As in the type species, the frontal forms vertical extensions which enwrap the preorbital region of the braincase; this feature is clearly displayed in AS.19.1. The maxilla is displayed in the type specimen (Fig. 35); it closely resembles that of *H. angularis*.

The dentary teeth are much broader and less tall than those of the type species; a row of ten is visible in AS.19.1. The oral border of the dentary rises steeply to form the pointed apex of the coronoid process (Fig. 35). The ventral border of the dentary forms a wide, open groove for the mandibular sensory canal as usual.

Two ossifications are visible on the hind border of the coronoid process. The larger, upper, element is the surangular and the lower the articular.

The angular is large; its suture with the dentary is approximately straight on the lateral surface of the coronoid process while above the sensory canal the angular forms the usual prolongation anteriorly. The deep posterior edge of the angular below the jaw articulation is capped by the retroarticular.

Of the palate only the quadrate is well known. The posterodorsal edge of this bone is rounded and just touches the metapterygoid. The articular condyle is broad, rounded and supported laterally by the quadratojugal, which is broad, tapering to a point immediately beyond the edge of the quadrate. The anterior head of the bone fits very closely against the quadrate behind the condyle, but no fusion is evident. As in *Propterus elongatus* a small notch occurs near the distal end of the quadratojugal. As in other macrosemiid genera, a lateral flange is present on the hyomandibular (AS.19.1).

(ii) Branchial arches. A few long, slender, pharyngeal teeth are exposed in the type specimen beneath the opercular. These contrast with the stout pharyngeal teeth known in *Macrosemius.*

(iii) Dorsal and anal fins. The anal fin is preserved in 1887.5.22. As in *Propterus* the fin-ray bases are closely set. The leading ray, which bears large fringing fulcra, is the longest, extending below the caudal fin; succeeding rays are progressively shorter.

The same specimen displays the dorsal fin, which is in two parts. The anterior part consists of about ten rays; it is high anteriorly, with a concave edge. The leading ray is very long, extending for a distance about equal to the depth of the trunk. It is closely followed by the second ray; the succeeding rays are more widely spaced. The anterior rays branch profusely so that the distal parts of the rays are formed entirely from thin filaments of bone. There are seven stout basal fulcra (Schultze 1966 : text-fig. 15) followed by long, deeply overlapping fringing fulcra which extend along the entire length of the leading ray.

The posterior dorsal lobe is composed of about 11 rays and is convex in outline; it is separated from the anterior part of the fin by a distance equal to the width of three scales.

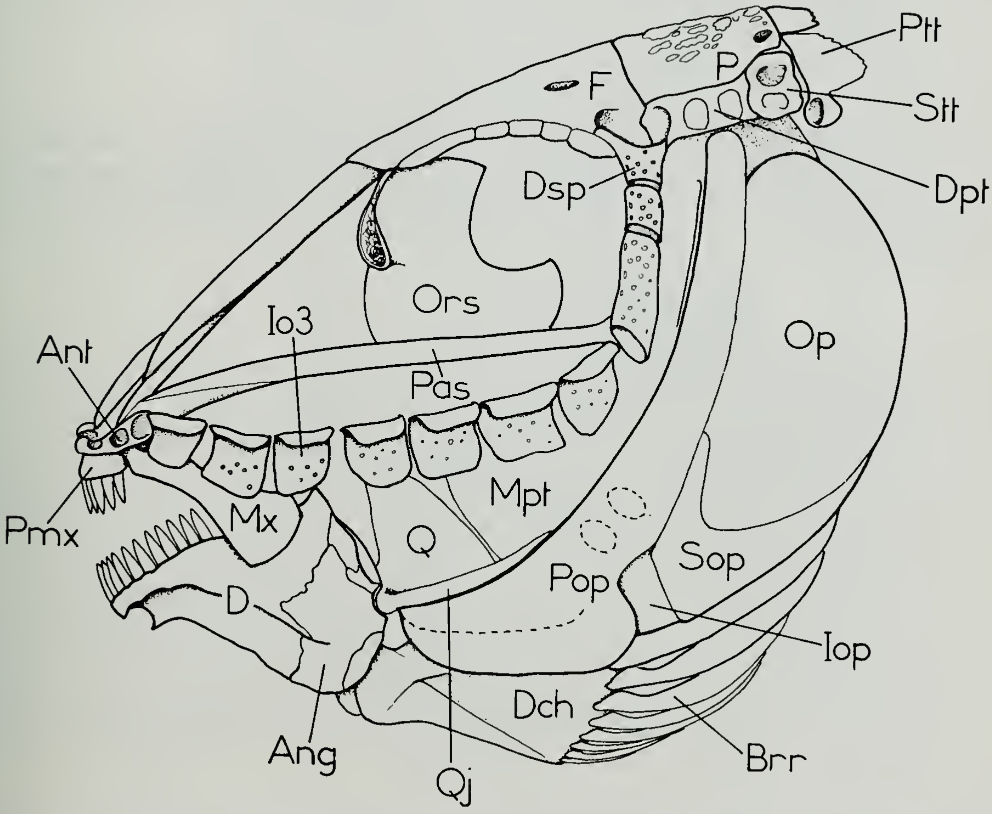

Fig. 36 *Histionotus oberndorferi* Wagner. Skull, with infraorbitals and roof restored from *H. angularis* Egerton. ×4½ approx.

(iv) Squamation. The trunk scales are similar in form, number and arrangement to those of the type species. The squamation flanking the dorsal fin of specimen AS.19.1 has been drawn and described by Schultze (1966 : 258, text-fig. 15). His observations and comments are repeated here.

The greater part of the dorsal fin is flanked by very deep scales some of which bear the pits of the dorsal lateral line on their surfaces. The lower part of the hind edges of these scales bear small pectinations, similar to those on the scales below them. The upper part of the scale, however, widens and the trailing edge of this region bears large pectinations. Beneath the basal fulcra of the dorsal fin, the uppermost longitudinal row is replaced by two rows, together equalling it in depth. The scales of the lower row, which bear the anterior pits of the dorsal lateral line, resemble the regular body scales, whereas those forming the upper row, alongside the fin, are small and taper posteriorly to form large pectinations. Schultze (1966 : 259) suggests that the row of deepened scales flanking the greater part of the length of the dorsal fin is the result of fusion between the small triangular scales and the regular longitudinal row which bears the dorsal lateral line.

Histionotus falsani Thiollière 1873

1873 *Histionotus falsani* Thiollière : 14; pl. 5, fig. 1.
1895 *Histionotus falsani* Thiollière; Woodward : 175.
1914 *Histionotus falsani* Thiollière; Eastman : 364; pl. 49, fig. 1.
1914 *Notagogus ornatus* Eastman : 366 (*partim*, specimen 4071 only).
1949 *Histionotus falsani* Thiollière; Saint-Seine : 208, fig. 92.

DIAGNOSIS. *Histionotus* reaching a standard length of about 150 mm; mean proportions as percentage of standard length: head length 32%, trunk depth 40%, predorsal length 39%, prepelvic length 60%, preanal length 81%; dentary teeth tall, conical.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.232.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. ML: 15.232, 15.239, 15.758; CM: 4071, 4077.

REMARKS. *H. falsani* is a rare, poorly known species. The fullest description is that given by Saint-Seine (1949 : 208, fig. 92) on which little improvement can be made while no specimens are available for acetic acid preparation. Although it does not appear to differ significantly from the type species in its proportions, the species is maintained here until more details of its structure become known.

Genus *NOTAGOGUS* Agassiz 1835

DIAGNOSIS. Small, fusiform macrosemiid fishes; skull-roof bones covered with an even layer of ganoine; sensory canals on skull of small diameter and completely enclosed in bone; fronto-parietal suture slightly sinuous; dermopterotic very large, housing the lateral part of the supratemporal commissure; supratemporal absent; supraorbitals forming one or two rows; dermosphenotic incorporated into skull roof; maxillary expansion asymmetrical, deep with straight oral border and convex upper and hind edges, maxillary teeth small, stout, forming a long row; dentary moderately curved, bearing small, stout teeth; anterodorsal edge of metapterygoid forming an acute angle; ectopterygoid bearing a row of small teeth; anterior border of preopercular forming a regular curve, ventral arm not greatly deepened, surface of opercular covered with a smooth layer of ganoine; pectoral fin with about 16 rays; pelvic fin comprising about six rays, fringing fulcra present; base of anal fin moderately extended, basal and fringing fulcra present; dorsal fin divided, each lobe with low convex profile; caudal fin with five or six axial lobe rays, weakly forked; squamation complete, forming a pattern of deepened hexagons, hind edges of scales pectinated, ganoine covering absent on ventral scales, which tend towards cycloidy; vertebral centra forming from dorsal and ventral crescents which fuse into complete cylinders in the anterior part of the trunk.

TYPE SPECIES. *Notagogus pentlandi* Agassiz (1835).

INTRODUCTION. The genus *Notagogus* was established by Agassiz (1835) to include four species

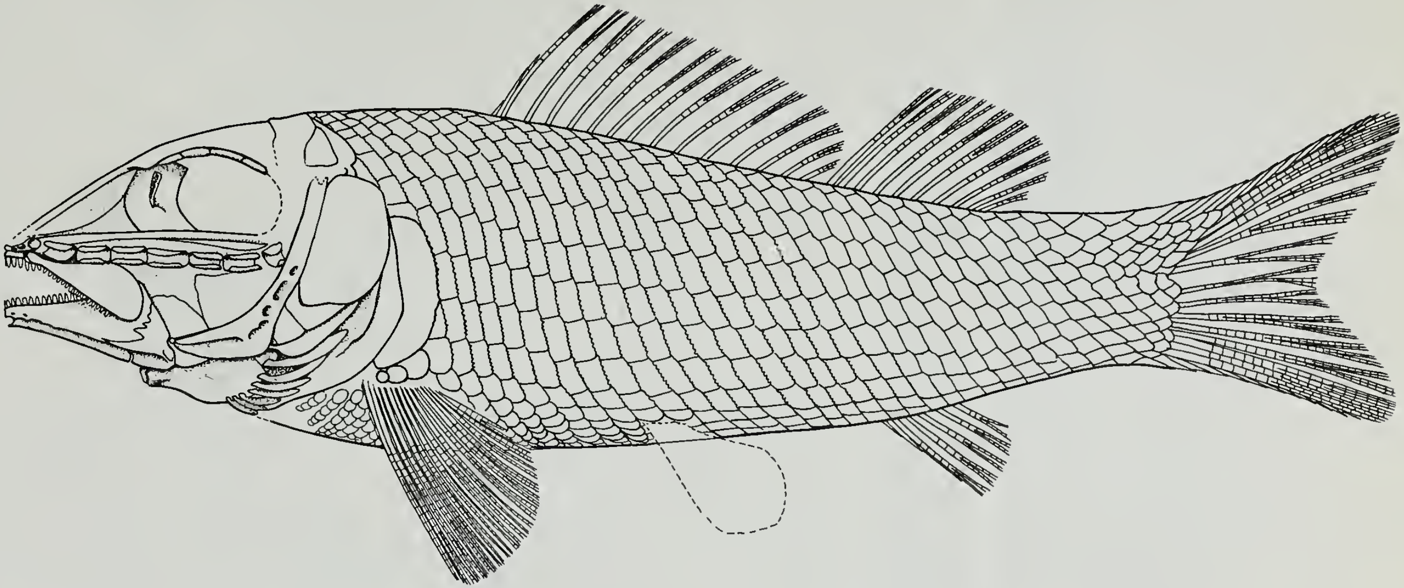

Fig. 37 *Notagogus denticulatus* Agassiz. Restoration of skeleton. × 1½ approx.

of small fusiform fishes with divided dorsal fins. These were *N. zieteni* and *N. denticulatus* from the Lower Kimmeridgian of Bavaria, and *N. pentlandi* and *N. latior* from the Lower Cretaceous of Torre d'Orlando, Italy. Thiollière (1873) described *N. inimontis* and *N. margaritae* from the Lower Kimmeridgian of Cerin and Vetter (1881) added *N. macropterus*.

Woodward (1895) grouped several species, ascribed by Costa (1850, 1853, 1864) to various species of *Notagogus* and *Blenniomoeus*, in *N. pentlandi*. He also referred *N. latior* Agassiz to this species, and transferred *N. zieteni* to *Propterus microstomus*. A new species, *N. parvus* from the Wealden of Bernissart, was described by Traquair (1911), and Eastman (1914, 1917) added *N. decoratus* and *N. minutus* from Bavaria, and *N. ornatus* from Cerin, to the genus.

In his revision of the Cerin fishes, Saint-Seine (1949) gave a detailed account of *N. inimontis* Thiollière. Wenz (1964) published a preliminary description of *N. ferreri* from the Neocomian of Santa-Maria-de-Meya, Spain.

REMARKS. Thiollière (1850, 1873) drew and gave a short description of a small macrosemiid which he named *Macrosemius helenae*. Saint-Seine (1949) later gave a full description of this species, retaining it within that genus since he believed that the dorsal fin was single. In fact this species is synonymous with *N. margaritae* Thiollière (1858), which thus becomes *N. helenae* (Thiollière 1850).

N. macropterus Vetter (1881) belongs to *Propterus elongatus*, and the type specimen (CM 5114) of Eastman's (1914) *N. ornatus* belongs to *N. inimontis*. Eastman referred two other specimens to his *N. ornatus*; CM 4660 also belongs to *N. inimontis*, and CM 4071 is a specimen of *Histionotus falsani* Thiollière.

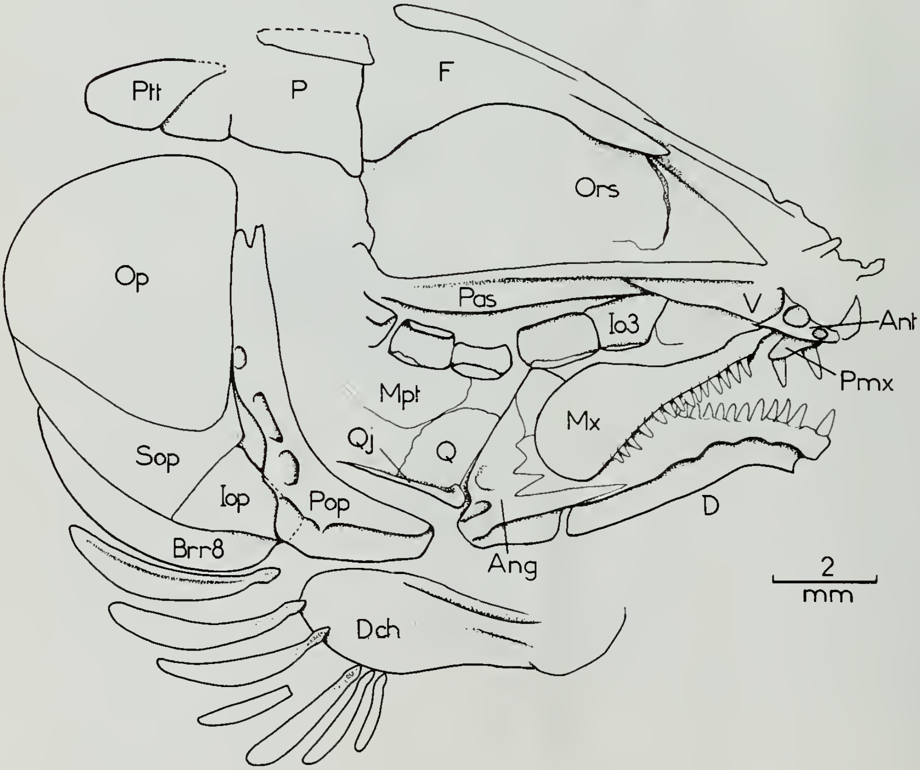

Fig. 38 *Notagogus denticulatus* Agassiz. Skull, as preserved in P1090.

Notagogus denticulatus Agassiz 1839

Figs 37–40

1839 *Notagogus denticulatus* Agassiz, **2** : pl. 50.
1844 *Notagogus denticulatus* Agassiz, **2**, 1 : 294; 2 : 289.
1851 *Notagogus denticulatus* Agassiz; Wagner : 65.
1863 *Propterus denticulatus* (Agassiz) Wagner : 646.
1881 *Notagogus denticulctus* Agassiz; Vetter : 43.
1895 *Notagogus denticulatus* Agassiz; Woodward : 187.
1917 *Notagogus minutus* Eastman : 287; pl. 14, fig. 4.

DIAGNOSIS. *Notagogus* reaching standard length of 70 mm; mean proportions as percentage of standard length: head length 33%, trunk depth 29%, predorsal length 41%; dorsal fin-ray count: ant. 10–14, post. 10–11; about 34 lateral line scales, only part of their hind borders bearing prominent serrations; no free fulcra on pectoral fin, very few fringing fulcra on first dorsal fin, fringing fulcra on anal fin.

HOLOTYPE. Bayerische Staatssammlung für Paläontologie und historische Geologie, München, AS.1.768.

HORIZON AND LOCALITIES. Lower Kimmeridgian of Eichstätt and Kelheim regions of Bavaria, Germany.

MATERIAL. BM(NH): P1090, P1089, P3610-11; Mü: AS.1.768; Ei: E1937-70; DM: S43 (photograph only examined).

DESCRIPTION. (i) General. *N. denticulatus* has the small size and regularly fusiform body typical of the genus. Proportional measurements, based upon three of the specimens, are given above. The following account applies largely to P1090, an immature specimen developed in acetic acid (Fig. 38).

(ii) Skull-roof and braincase. The structures are poorly preserved in the specimens; those of *N. helenae* and *N. inimontis* are described below (pp. 196–8, 200).

(iii) Circumorbital series. The supraorbitals remain unknown. The antorbital forms the usual tapering tube around the anterior part of the infraorbital sensory canal (Fig. 38). Two large pores in the lateral wall are visible. Infraorbitals 3–7 are present in the specimen. These form delicate scrolls around the upper and lower borders of the infraorbital sensory canal; they are perforated by fine pores. The last two infraorbitals, behind the eye, are not preserved.

(iv) Hyopalatine bones. The quadrate and the lower part of the metapterygoid are visible; both have corrugated surfaces. These two bones, and the quadratojugal, are better known in *N. inimontis.*

(v) Dermal upper jaw. Two of the tall, conical premaxillary teeth are visible (Fig. 38). The remainder of the premaxilla remains unknown.

The maxilla forms a slender cylindrical shaft behind the medial process. The ventral surface of the shaft is raised into a bulge. The dorsal border is convex and continues into the rounded hind border of the bone. The oral border is slightly concave and bears about 15 small, stout teeth which extend onto the cylindrical part of the maxilla; the teeth increase in height anteriorly.

(vi) Lower jaw. The mandible in this genus is long, extending about half of the length of the skull. The coronoid process is broad and shallow and the curvature of the ventral border of the dentary is less marked than it is in other macrosemiid genera.

The mandibular sensory canal entered the angular below a slender arch of bone as in *Propterus.* It continued forward, as usual, through a wide trough along the ventral parts of the angular and dentary.

The angular extends along the lower half of the posterior border of the coronoid process. The surangular appears to form the greater part of the dermal coronoid process, although most of the bone is hidden by the maxilla in the specimen and its complete outline cannot be followed. The suture between the dentary and angular follows a long zigzag course, the angular forming a long tapering process anteriorly along the dorsal edge of the sensory canal as usual. The dentary

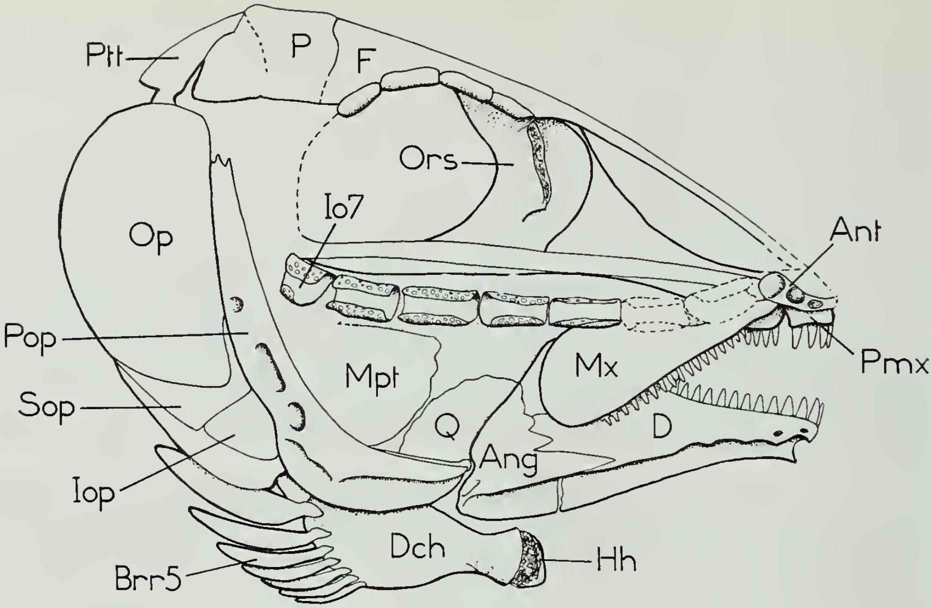

Fig. 39 *Notagogus denticulatus* Agassiz. Restoration of skull. ×6 approx.

bears a row of about 12 closely-set teeth intermediate in size between those of the maxilla and premaxilla.

(vii) Preopercular, hyoid arch and branchiostegal series. The anterior edge of the preopercular forms a smooth curve. The dorsal arm falls short of the skull-roof and the ventral arm ends at the level of the quadrate articulation as usual. As in other macrosemiids the preopercular sensory canal was exposed by two large fenestrae in the lower part of the upper arm. The ventral arm too has the typical macrosemiid form (Fig. 38).

The opercular is as deep as it is broad in the young specimen (P1090); in older specimens it becomes proportionally narrower. The subopercular is large and deeply embayed along the suture with the opercular. The suture between the subopercular and interopercular is long and straight as usual. The anterior end of the latter is remote from the mandible as in all other members of the family. The hyomandibular is not exposed in the specimens.

The proximal ceratohyal is partially visible in P1090; it is less deep posteriorly than it is in other macrosemiids. This specimen also displays the eight branchiostegal rays; these are similar in form and arrangement to those of *Macrosemius*. The blade of the uppermost ray is deeper than those of the remainder and appears to have been attached to the operculum and not to have articulated with the ceratohyal.

(viii) Vertebral column. The axial skeleton remains unknown in this species; it is described in other members of the genus below.

(ix) Pectoral girdle and fin. The pectoral girdle is not clearly preserved in the specimens. It seems to resemble that of *N. helenae* described below.

The fin consists of about 15 rays. The leading ray, compound in origin, is well preserved in P1090 (Fig. 40A), and is formed mainly from a long unfused pair of branching, segmented hemitrichs resembling those of the succeeding rays. The basal part of the dorsal hemitrich is produced into a short basal process, and appears to be fused to the endoskeletal propterygium. A shorter ray, also with a dorsal process, is fused along one-third of the unsegmented part of the major lepidotrich, its sharp tip projecting freely. Two small spines occur above this point on the major ray; these are probably fused fringing fulcra.

(x) Pelvic fin. The fin was supported by at least four rays, of which the first is preceded by basal and fringing fulcra.

(xi) Dorsal and anal fins. The dorsal fin is divided into two lobes of approximately equal height; this contrasts with the condition in *Histionotus* and *Propterus* where the anterior lobe is the taller. There are about 14 anterior rays preceded by three basal and about one fringing fulcrum. The last three rays of the lobe decrease rapidly in height to form a rounded hind border. The posterior lobe comprises nine or ten rays, more closely set than those of the anterior part. All the dorsal fin-rays are segmented and branch once.

The anal fin consists of about four rays, the first bearing fringing fulcra. None of the rays is markedly long, and the base of the fin is not compact, in contrast to the condition in *Propterus* and *Histionotus*.

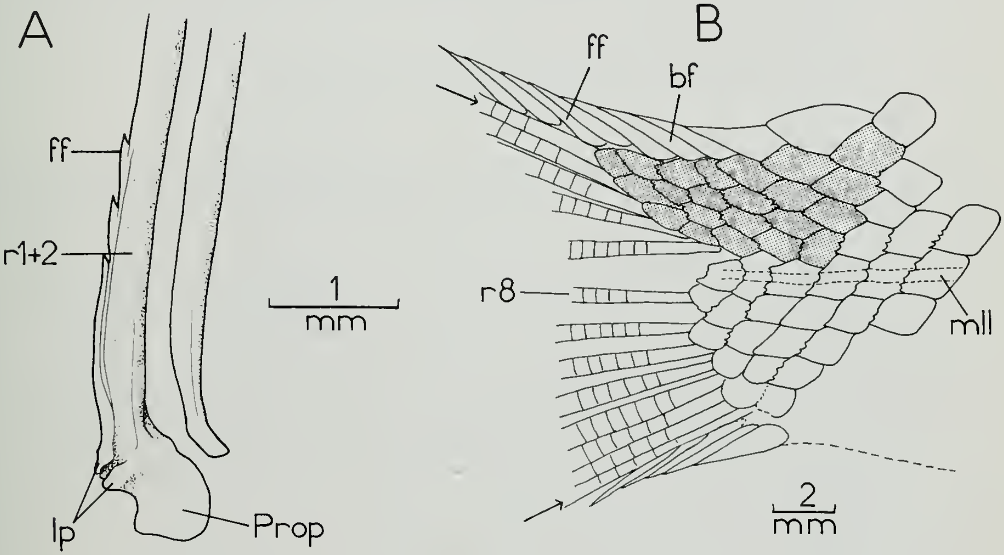

Fig. 40 *Notagogus denticulatus* Agassiz. A, leading rays of right pectoral fin of P1090. B, caudal squamation, as preserved in AS.1.768, axial lobe shaded. Arrows indicate outermost fin-rays.

(xii) Caudal fin. This is preserved in AS.1.768; it is weakly forked. The axial lobe bears five rays; as usual eight rays occur below these. As in *Propterus* and *Histionotus* the axial lobe rays supported the upper lobe of the fin. Both leading edges of the fin bear fringing fulcra. The axial lobe squamation is shown in Fig. 40B.

(xiii) Squamation. There are four postcleithral scales; the uppermost is very deep, extending along the dorsal arm of the cleithrum. The remaining three lie in a row above the insertion of the pectoral fin; they are small, circular and decrease in size anteriorly.

There are about 34 lateral line scales, and about 14 scales in the transverse rows in the anterior part of the body. The prominent serrations on the posterior edges of the scales are restricted to the part overlapping the succeeding scale in the same longitudinal row. Thus in the deepest scales, behind the skull, about one-fifth of the hind border is smooth.

In the ventral region between the pectoral fins the scales form a cycloid pattern similar to that described in *Propterus microstomus* (AS.1.768).

Notagogus helenae (Thiollière 1850)

Fig. 41

1850 *Macrosemius helenae* Thiollière : 135.
1858 *Notagogus margaritae* Thiollière : 783.
1873 *Macrosemius helenae* Thiollière; Thiollière : 14; pl. 6, fig. 2.
1873 *Notagogus margaritae* Thiollière; Thiollière : pl. 6, fig. 4.
1883 *Macrosemius helenae* Thiollière; Sauvage : 478.
1949 *Macrosemius helenae* Thiollière; Saint-Seine : 193, text-figs 84–86; pl. 20B, C.

DIAGNOSIS. *Notagogus* reaching 100 mm standard length; mean proportions as percentage of standard length: head length 32%, trunk depth 28%, predorsal length 33%; dorsal fin-ray counts: ant. 15, post. 10–12; about 38 lateral line scales, their entire hind borders bearing small serrations; two lobes of dorsal fin closely spaced; fringing fulcra on anal and caudal fins only.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.220.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. LM: 15.208, 15.220, 15.223, 15.224, 15.230, 15.231, 150.752, 150.875, 15.406, 150.756; L: AC.1874-543.

REMARKS. Thiollière (1850) named two small species of macrosemiid from Cerin, *Macrosemius helenae* and *Notagogus inimontis*. In his posthumous publication of 1873 there were lithographs of these two species (pl. 6, figs 2, 3), and of another of similar shape and size, *N. margaritae* (pl. 6, fig. 4). He left no description of the latter.

Thiollière and later Saint-Seine (1949) maintained that *M. helenae* possessed a long, undivided dorsal fin and hence was correctly ascribed to this genus, but there are several points of dissimilarity between *M. helenae* and the type species of *Macrosemius* which call this observation into question. Thus *M. helenae* differs from *M. rostratus* in having, for example, a forked caudal fin, a complete covering of scales with no intervening scale-rows and a full row of maxillary teeth.

Thiollière's *M. helenae* greatly resembles *Notagogus margaritae* in form and size and in the total number of dorsal fin-rays (about 26). Saint-Seine (1949 : 204) maintained that the dorsal fins of Thiollière's specimens of *N. margaritae* were single, and thus transferred them to *M. helenae*. However, the full outline of the dorsal fins of these two species is seldom preserved; usually only the unsegmented proximal parts of the rays have survived. Since the rays exhibit an even width throughout the length of the fin, it is difficult to ascertain whether the fin was divided or not if the two lobes were placed close together.

Re-examination of the specimens has shown that in fact those referred to *M. helenae* by Saint-Seine possess divided dorsal fins and are wrongly ascribed to *Macrosemius*. Thus in 15.223 and 15.224 (included by Thiollière in *N. margaritae*) there is a slight change in inclination between the 15th and 16th dorsal fin-rays indicating that the two rays belonged to separate fin webs, although there is no appreciable change in the spacing between them. In the other four specimens listed by Saint-Seine (1949 : 194), the bases lie flat. In 150.756 too there is a change in inclination between the 15th and 16th rays, and in 150.875, an immature specimen of 25 mm standard length, in which the full outline of the fin is preserved, there is unquestionably a separate anterior lobe supported by 15 rays.

Thus the specimens listed above are here taken to belong to *N. helenae*; all of them possess 15 anterior dorsal fin-rays and between 10 and 12 posterior dorsal fin-rays. This species differs from the type species *N. pentlandi* in possessing a greater number of dorsal fin-rays, a smaller predorsal length and a more obtuse snout profile.

DESCRIPTION. (i) Skull roof and braincase. The state of preservation of the material has led to several inaccuracies in the description given by Saint-Seine (1949 : 193–199). A full redescription is given below.

The sensory canals of *Notagogus* differ from those of other macrosemiids in being comparatively narrow; they are completely surrounded by bone and not exposed by large fenestrae.

Saint-Seine (1949 : fig. 84) misunderstood the structure of the preorbital region of the frontals; he considered that these ended above the front of the orbit and that the ethmoidal region was devoid of a dermal bone covering. In fact the frontals form the usual trough for the supraorbital sensory canal in this region. There is no sound evidence, either, for the kidney-shaped nasals of Saint-Seine's description.

The parietals are large, roughly triangular bones. The anterior border, which corresponds to the greatest width, is overlapped by the frontal along a slightly sinuous suture. The anterolateral border of the parietal forms a short suture with the dermosphenotic. The posterolateral border forms two large embayments as it converges towards the midline; in contrast with other members of the family, the parietal enclosed only a very short section of the supratemporal commissure on either side of the midline. The surface of the bone is covered with an even layer of ganoine which is interrupted by the anterior and middle pit-lines. The middle pit-line forms a short groove close to, and parallel with, the posterior edge of the parietal. The anterior pit-line is equally short, extending at an angle of about 100 degrees anterolateral to the middle pit-line (Fig. 41). There is no evidence to suggest that a branch of the supraorbital sensory canal extended onto the parietal (cf. Saint-Seine 1949 : fig. 84).

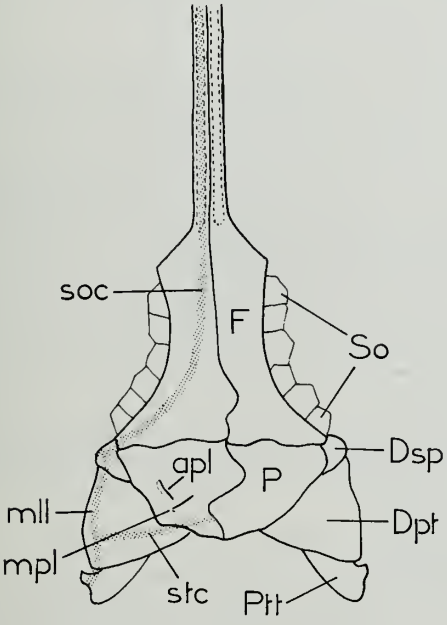

Fig. 41 *Notagogus helenae* (Thiollière). Skull roof, as preserved in 15.220. × 6.

Saint-Seine (1949) identified two bones in contact with the posterolateral border of the parietal: a 'supratemporal' (i.e. dermopterotic) suturing with the anterior embayment, and an 'extrascapular' (i.e. supratemporal) posteriorly. This region of the skull, however, is in fact occupied by a single, large, triangular bone; Saint-Seine has mistaken for a suture the collapsed tube of the lateral part of the supratemporal commissure which passed through this element. This condition is unknown in other macrosemiids. Since this bone houses both the supratemporal commissure and the cephalic division of the main lateral line, it could be the dermopterotic, the supratemporal, or the result of the fusion of both. The supratemporal is reduced in all macrosemiids and may have disappeared in *Notagogus*, its place and sensory canal taken by the dermopterotic. Alternatively, since fusion has perhaps occurred between the parietal and the medial supratemporal (see p. 143), fusion between the lateral supratemporal and the dermopterotic may have occurred also. The bone is labelled dermopterotic in Fig. 41.

The dermosphenotic is described here since it is fully incorporated into the skull-roof, unlike its condition in other members of the family. It forms a short posteromedially-directed process between the dermopterotic and parietal. Although the full outline of the bone is not exposed in the specimens, the bone clearly enclosed the point of fusion between the infra- and supraorbital sensory canals.

The parasphenoid is, as usual, stout and straight. A small basipterygoid process is visible beneath the ascending process of the parasphenoid in 15.220. A shallow groove, which, as Saint-Seine suggested (1949 : 196), may have held the efferent pseudobranchial artery, passes along the bone above the basipterygoid process.

A large orbitosphenoid surmounts the parasphenoid about midway along its length. Its posterior edge is deeply concave and a lateral flange projects laterally along the anterior limit of the orbit, as in *Propterus* and *Macrosemius*. The anterior border of the bone is straight and vertical.

(ii) Circumorbital series. Unlike the condition in other members of the family, there appear to be two rows of supraorbitals. These are small and polygonal in shape, as described by Saint-Seine (1949 : 194, fig. 85).

The remains of infraorbitals 2–7 are preserved in 15.223; they are of similar shape and size to those of *Notagogus denticulatus* and Saint-Seine's (1949 : 196, fig. 85) identification of three large infraorbital plates was mistaken. Also there is no evidence to indicate that the sclerotic was ossified.

(iii) Hyopalatine bones. The palate is exposed in 15.220. The straight edges of the indentation in the anterodorsal border of the metapterygoid form an angle of about 70 degrees; this contrasts with the condition in *Macrosemius* and *Propterus* where this angle is obtuse. The anteroventral border of the metapterygoid forms a long straight suture with the quadrate.

The anteroventral border of the quadrate is excluded from the oral border of the palate as usual by a long extension of the ectopterygoid which reaches almost to the jaw articulation (Saint-Seine 1949 : 196, fig. 85). The ectopterygoid bears a long row of very small hemispherical teeth along its thickened oral border. The endopterygoid forms a long gently curving suture with the ectopterygoid, its medial edge lying alongside the parasphenoid.

The relationship between the quadrate and the quadratojugal is more certainly known in *N. inimontis*, described below.

(iv) Dermal upper jaw. The maxilla resembles that of *N. denticulatus* in having a ventral thickening on the shaft and in the form of the posterior expansion (15.223). The teeth, however, are fewer, and are restricted to the maxillary expansion.

The premaxilla is visible in 15.220. The nasal process is long and stout, and contacts the dorsal surface of the braincase. The dentigerous head of the bone bears about four stout tapering teeth, each about four times the size of those on the maxilla.

(v) Lower jaw. The posterior edge of the coronoid process arises much more steeply than does that of *N. denticulatus* (15.208). The dentary supports about ten teeth, slightly larger than those on the premaxilla. The greater part of the dermal coronoid process is formed by the dentary; this bone forms a long suture with the angular, curving anteroventrally. The surangular remains unknown. The region of the mandible enclosing the sensory canal is not preserved in the specimens.

(vi) Preopercular, hyoid arch and opercular series. The preopercular is crescent-shaped, with the dorsal arm slightly longer than the ventral arm. The latter is not as deep as that of *N. denticulatus*. At least two fenestrae are present in the lateral wall of the sensory canal in the region of the greatest curvature of the bone (15.208).

The opercular (15.220) is deeper than broad, with a smoothly curved trailing edge. The subopercular is similar to that of *N. denticulatus*; it forms a straight suture with the interopercular which as usual is small and, contrary to the opinion of Saint-Seine (1949 : 197), does not resemble a branchiostegal ray.

There are seven or eight branchiostegals, similar to those of *N. denticulatus*.

(vii) Vertebral column. The feebly-ossified vertebral column has been described by Saint-Seine (1949 : 198, fig. 86) in specimens 15.231 and AC 1874-543. In the abdominal region there are large, crescentic, dorsal and ventral hemicentra; each dorsal hemicentrum is in contact with, and slightly in advance of, its ventral partner. The neural and haemal arches rested on the notochord in the gaps between the hemicentra. The ventral crescents decrease in size in the caudal region and the bases of the haemal arches enlarge and spread around the notochord. The neural arches are paired as usual but do not articulate with the proximal dorsal fin radials as suggested by Saint-Seine (1949 : 198).

(viii) Pectoral girdle and fin. The post-temporal is of the usual triangular shape, with a broad canal in the lateral border which housed the main lateral line. The supracleithrum is large and forms a wide, anterodorsally-facing, funnel-shaped opening for the exit of this canal. The cleithrum is a broad, gently curving bone; it is wider than that drawn by Saint-Seine (1949 : fig. 85) since it comprises the piece he mistook for an anterior postcleithral scale. The anterior and posterior borders of the cleithrum are smoothly convex. Two vertical rows of denticles are present on the lateral surface.

The endoskeleton of the fin remains unknown. There are at least 10 pectoral fin-rays; no fringing fulcra are preserved.

(ix) Pelvic fin. The pelvic fin consists of five rays; no fringing fulcra are present.

(x) Dorsal and anal fins. As discussed above, the dorsal fin is divided, contrary to the views of Thiollière (1873) and Saint-Seine (1949 : 199). The total number of dorsal fin-rays, about 26, is high for this genus. The anterior lobe is the longer, with 15 rays. The leading ray is preceded by two short basal fulcra; there are no fringing fulcra. The posterior lobe follows very closely behind the first, and both lobes are low and rectangular in outline. The dorsal fin radials are similar to those described in *Macrosemius* (15.231).

The anal fin is poorly preserved in the specimens; it is formed from five rays, of which the first bears fringing fulcra.

(xi) Caudal fin. The caudal fin comprises 14 rays, of which six emanate from the axial lobe. The axial lobe rays follow the typical macrosemiid pattern: the uppermost is continuous with the longest scale row, the following rays clasp the hypurals, and the lowermost, slightly separated from the others, clasps the tip of its hypural. Both leading edges of the fin bear fringing fulcra.

(xii) Squamation. There are about 36 lateral line scales and 11 in the deepest transverse row. The hind borders of the flank scales are convex and, in contrast to the condition in *N. denticulatus*, bear serrations along their entire length. The ventral scales, between the paired fins, are cycloid (15.231).

There are four postcleithral scales, decreasing in depth ventrally; their hind borders are smooth. The large anterior postcleithral scale drawn by Saint-Seine (1949 : fig. 85) is in fact part of the cleithrum, as explained above.

Notagogus inimontis Thiollière 1850

Fig. 42

1850 *Notagogus Imi montis* Thiollière : 137.
1858 *Notagogus iunismontis* Thiollière : 783 (name only).
1873 *Notagogus inimontis* Thiollière; Thiollière : 15; pl. 6, fig. 3.
1893 *Notagogus inimontis* Thiollière; Sauvage : 428.
1895 *Notagogus inimontis* Thiollière; Woodward : 188.
1914 *Notagogus inimontis* Thiollière; Eastman : 365; pl. 49, fig. 2; pl. 50, figs 1, 2.
1914 *Notagogus ornatus* Eastman : 366; pl. 50, fig. 3 (*partim*, specimens 5114, 4660 only).
1949 *Notagogus inimontis* Thiollière; Saint-Seine : 205, text-figs 90, 91.

DIAGNOSIS. *Notagogus* reaching standard length of 90 mm; mean proportions as percentage of standard length: head length 36%, trunk depth 27%, predorsal length 43%; dorsal fin-ray count: ant. 10–13, post. 10; about 34 lateral line scales, their entire borders bearing small serrations; all fins bearing fringing fulcra.

HOLOTYPE. Muséum d'Histoire Naturelle, Lyon, 15.242.

HORIZON AND LOCALITY. Lower Kimmeridgian of Cerin, Ain, France.

MATERIAL. LM: 15.420, 15.416, 15.242, 15.250, 15.249, 15.409; CM: 5114, 5115, 5116, 4418, 4654.

REMARKS. This species bears a strong resemblance to *N. denticulatus* in its body proportions and fins. Nevertheless it is not always easy to distinguish from *N. helenae* in the Cerin fauna, and thus the dissimilarities between these two are stressed below.

DESCRIPTION. (i) Skull-roof and braincase. The skull-roof is very similar to that of *N. helenae* (Saint-Seine 1949 : fig. 90); it is displayed in 15.249. Saint-Seine thought, wrongly, that the frontals did not extend laterally over the sides of the ethmoidal region; in fact they do so, as in *Histionotus*.

As in *N. helenae* the parietal is flanked by a single large bone which Saint-Seine, probably correctly, identified as the 'supratemporal' (= dermopterotic). There is no evidence to support the presence of a narrow bone identified as the 'extrascapular' (= supratemporal) by Saint-Seine (1949 : figs 90, 91).

The dermosphenotic is fully incorporated into the skull roof as in *N. helenae* (CM 5114). The infraorbital sensory canal entered the bone through a ventrally-directed pore and joined the supratemporal canal within it.

(ii) Circumorbital bones. A single row of four small polygonal supraorbitals is present along the orbital embayment of the frontals (Saint-Seine 1949 : figs 90, 91). The infraorbitals are not preserved in any of the specimens.

(iii) Hyopalatine bones. The metapterygoid and quadrate are visible in CM 5114, and are very similar to those of *N. helenae*. The quadrate articulation with the mandible is stout and deep. The quadratojugal lies in its usual position along the upper edge of the preopercular (Fig. 42). Anteriorly the bone forms a stout rod fitting closely behind the ventrolateral part of the quadrate condyle; no fusion between the two bones is evident, although it may have occurred. The posterior part of the bone is, unusually, expanded over the ventrolateral surface of the metapterygoid.

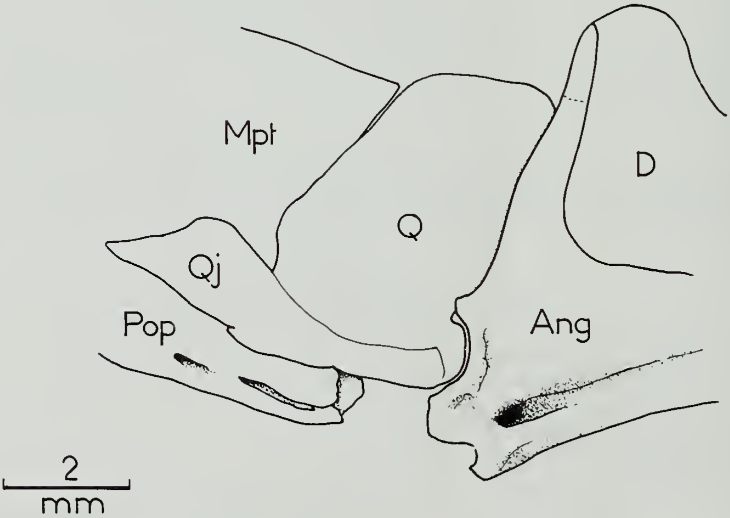

Fig. 42 *Notagogus inimontis* Thiollière. Region of right jaw articulation of CM 5114.

(iv) Dermal upper jaw. The premaxilla bears several stout teeth. The lower part of the nasal process is visible in 15.249, as Saint-Seine noted (1949 : 206, fig. 91).

The posterior expansion of the maxilla is deeper than that of *N. helenae*. The oral border is straight and bears more teeth (about 20) than that of *N. helenae*, extending onto the anterior, cylindrical part of the bone. The teeth are small and peg-like (15.416).

(v) Lower jaw. The mandible, preserved in 15.416 and CM 5114, closely resembles that of *N. helenae*.

(vi) Preopercular, hyoid arch and opercular series. The anterior edge of the preopercular forms a regular arc from the skull-roof to the jaw articulation (CM 5114); it is not sharply bent as described by Saint-Seine (1949 : fig. 91). Two fenestrae occur in the canal in the lower part of the dorsal arm as usual (15.242).

The opercular is deeper than broad, with a smoothly rounded trailing edge (cf. Saint-Seine 1949 : fig. 91); its surface is covered by an even film of ganoine. The remaining opercular and branchiostegal bones, as far as can be determined from the specimens, resemble those of *N. denticulatus.*

The distal ceratohyal is exposed in several specimens. It is thickened dorsally, becoming very stout as it tapers anteriorly. It forms a thin ventral expansion for the articulation of the branchiostegals, as usual.

(vii) Vertebral column. The vertebrae are exposed in a small specimen (CM 5115) of standard length 70 mm. These form complete cylinders in the abdominal region. Where the smooth outer surfaces of the centra have been removed, vertical, fibrous striations are exposed; these indicate that the larger part of the centra was formed of ossification in the notochordal sheath.

(viii) Pectoral girdle and fin. The dermal pectoral girdle is not clearly exposed in any of the specimens. It appears to resemble that of *N. helenae.*

There are six proximal pectoral radials; the sixth, the longest, bears lateral flanges, as in *Macrosemius rostratus* (15.409). The fin comprises 17 rays, the leading ray bearing free fringing fulcra, in contrast to that of *N. denticulatus* (15.416, 15.242).

(ix) Pelvic girdle and fin. The pelvic basipterygium is preserved in 15.409; it is similar in shape to that of *Macrosemius.* Eight pelvic rays are visible in 15.249. The leading ray is preceded by three basal fulcra and bears fringing fulcra.

(x) Dorsal and anal fins. The dorsal fin of this species resembles that of *N. denticulatus* both in form and in the number of fin-rays. The anterior lobe of the fin, with about 12 rays, is about twice as long as the posterior part, in which the 10 rays are less widely spaced. Although the gap between the lobes is small, the discontinuity between them is obvious since the last rays in the anterior lobe are short and thin compared with those of the posterior lobe. This contrasts with the condition in *N. helenae* in which the rays are uniform throughout the two lobes. Also in contrast to *N. helenae* and *N. denticulatus,* the three basal fulcra at the base of the leading ray are followed by fringing fulcra, and the first ray of the posterior lobe is unsegmented, unbranched and much shorter than its successors.

The anal fin is composed of about five rays preceded by three unpaired basal fulcra and a series of deeply imbricated fringing fulcra.

(xi) Caudal fin. The caudal fin does not differ significantly from those of the other species of *Notagogus* described above.

(xii) Squamation. There are three postcleithral scales aligned in tandem along the posterior border of the cleithrum; the uppermost is largest and they decrease in size ventrally. Their hind borders are smooth.

There are about 34 lateral line scales and about 11 transverse scales at the deepest point of the trunk; the main lateral line passed through the fifth row from the dorsal midline. The hind border of the flank scales is serrated. The longitudinal row alongside the dorsal fin bears the pits of the dorsal lateral line on several of its scales, as in *Histionotus.*

The ventral squamation, cycloid as in other species of *Notagogus,* is exposed in CM 5114.

Notagogus pentlandi Agassiz 1835

1835 *Notagogus pentlandi* Agassiz **2** : pl. 49, fig. 2.
1835 *Notagogus latior* Agassiz **2** : pl. 49, fig. 3.
1844 *Notagogus pentlandi* Agassiz **2**, **1** : 10, 294.
1844 *Notagogus latior* Agassiz **2**, **1** : 10, 294.
1850 *Notagogus pentlandi* Agassiz; Costa : 312; pl. 5, fig. 2; pl. 7, fig. 5.
1850 *Notagogus erythrolepis* Costa : 314; pl. 4, figs 6, 7.

1850 *Notagogus minor* Costa : 315; pl. 5, fig. 4.
1850 *Blenniomoeus longicauda* Costa : 319; pl. 6, fig. 2.
1850 *Blenniomoeus brevicauda* Costa : 321; pl. 5, fig. 3.
1853 *Blenniomoeus major* Costa : 34; pl. 2, figs 4–6.
1864 *Notagogus pentlandi* Agassiz; Costa : 72; pl. 12, fig. 5.
1864 *Notagogus crassicauda* Costa : 74; pl. 12, figs 6, 7.
1864 *Blenniomoeus longicauda* Costa; Costa : 99.
1864 *Notagogus erythrolepis* Costa; Costa : 102; pl. 11, fig. 11.
1864 *Notagogus gracilis* Costa : 103; pl. 11, fig. 8.
1882 *Notagogus pentlandi* Agassiz; Bassani : 237, 239.
1895 *Notagogus pentlandi* Agassiz; Woodward : 186; pl. 3, figs 7, 8.

DIAGNOSIS. *Notagogus* reaching standard length of 115 mm; mean proportions as percentage of standard length: head length 36%, trunk depth 27%, predorsal length 45%; dorsal fin-ray count: ant. 14, post. 10; about 34 lateral line scales.

HOLOTYPE. British Museum (Natural History), 117.

HORIZON AND LOCALITY. Lower Cretaceous (Albian or Aptian) of Torre d'Orlando, Naples, Italy.

MATERIAL. BM(NH): 117, P2065, P6866, P1097a, b, c.

REMARKS. The available specimens reveal little detail, since the bones are largely shattered beyond recognition. This species is closely similar in fin form and body proportions to *N. denticulatus*, but until the squamation and fin fulcra are more fully known it seems reasonable to maintain the two species as separate, in view of their separation in time.

Three of the specimens (P1097a, b, c) are very small and there is no guarantee that they belong to *N. pentlandi*. They probably do, however, as the proportions of the head and the long dorsal fin differentiate them from other members of the Torre d'Orlando fauna.

DESCRIPTION. (i) Caudal fin. The adult condition is preserved in P2065. There are 14 rays of which six emerge from the axial lobe. The internal skeleton of the fin is shown in two of the juvenile specimens, P1097a (SL 44 mm) and P1097b (SL 54 mm). In P1097a, six supports articulated with six full-length ventral rays. Another two smaller, unsegmented rays occur below these, as in *Enchelyolepis*. These two rays would presumably have elongated to form the adult complement of eight lower rays. The condition in P1097b is similar; in both these specimens there are only four axial lobe rays.

(ii) Vertebral column. The axial skeleton is exposed in P1097c; it has been drawn by Woodward (1895 : pl. 3, fig. 8). In the caudal region each vertebral unit consists of a ventral crescent, fused to the haemal arch, and a dorsal crescent alongside the neural arch; this structure is similar to that described by Saint-Seine (1949) in *N. helenae*. In the anterior region the dorsal and ventral elements fuse to form ring centra, which also occur in *N. inimontis* and *N. denticulatus*.

(iii) Squamation. Contrary to Agassiz's (1844 : 294) opinion, the main body scales of *N. pentlandi* are rhomboid, although most of their hind edges are broken. In the young forms, however, the squamation is entirely cycloid (P1097); the scales are very similar to those of *Enchelyolepis* (Schultze 1966 : 276).

Notagogus parvus Traquair 1911

1911 *Notagogus parvus* Traquair : 26, pl. 4, fig. 10.

DIAGNOSIS. *Notagogus* attaining a standard length of 70 mm; mean proportions as percentage of standard length: head length 32%, trunk depth 32%; dorsal fin-ray counts: ant. 9, post. 11; scales cycloid.

HOLOTYPE. Specimen in the Musée Royale d'Histoire Naturelle, Bruxelles.

HORIZON AND LOCALITY. Wealden of Bernissart, Belgium.

MATERIAL. None examined.

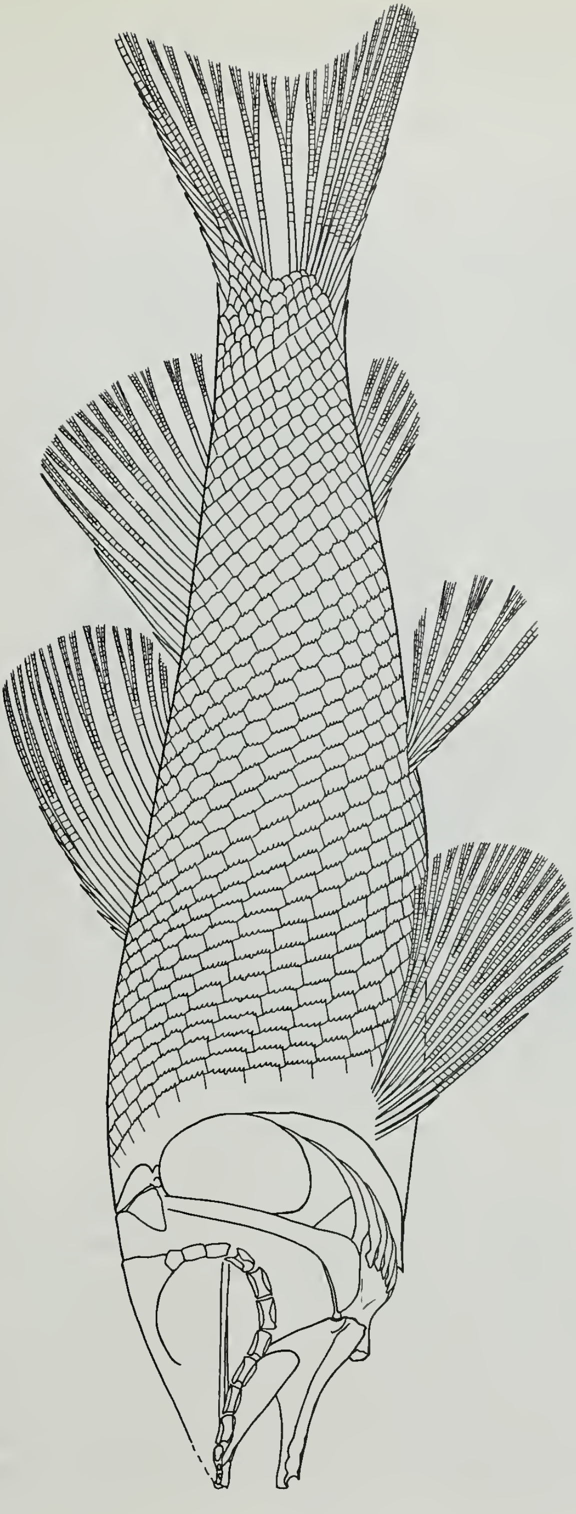

Fig. 43 *Notagogus decoratus* Eastman. Restoration of skeleton. ×2½ approx.

REMARKS. The material (eight specimens in the above Museum) is poorly preserved. The species is small (SL 70 mm) and is remarkable in possessing cycloid scales. As in *N. inimontis*, the vertebrae form complete rings.

Notagogus decoratus Eastman 1914

Fig. 43

1914a *Notagogus decoratus* Eastman : 360; pl. 7, fig. 3.

DIAGNOSIS. *Notagogus* attaining a standard length of 60 mm; mean proportions as percentage of standard length: head length 33%, trunk depth 22%, predorsal length 42%; dorsal fin-ray counts: ant. 9–10, post. 10–11; about 36 lateral line scales, only part of their hind borders bearing prominent serrations; no fringing fulcra on pectoral fin, a few on the dorsal and anal fins.

HOLOTYPE. Carnegie Museum, Pittsburgh, 5110.

HORIZON AND LOCALITY. Lower Kimmeridgian of Eichstätt region, Bavaria, Germany.

MATERIAL. CM 5110; specimen in Berger Museum, Blumberg near Eichstätt.

REMARKS. This species is reconstructed in Fig. 43. Although based upon a single small specimen, Eastman in describing this fish (1914a) was probably right to distinguish it from *N. denticulatus*, the other species of the genus occurring in Bavaria. It differs from *N. denticulatus* in its more elongated body, relatively larger pectoral fins and triangular dorsal fins.

Notagogus ferreri Wenz 1964

1964 *Notagogus ferreri* Wenz : 269, text-fig. 1; pl. 12b.

DIAGNOSIS. *Notagogus* reaching standard length of 30 mm; proportions as percentage of standard length: head length 30%, trunk depth 23%, predorsal length 39%; dorsal fin-ray counts: ant. 12, post. 11; 24 cylindrical vertebral centra; fringing fulcra present on caudal fin only.

HOLOTYPE. Specimen in the collection of L. Ferrer Condal.

HORIZON AND LOCALITY. Neocomian of Santa-Maria-de-Meya, Lerida, Spain.

MATERIAL. None examined.

REMARKS. This species is remarkable for its small size (total length 35 mm), although the single known specimen may be immature. Unlike other members of the genus, the centra are fully ossified rings throughout the column.

The trailing edge of the caudal fin is only slightly concave; it was supported by 10 rays, of which only six appear to form the lower lobe. This contrasts with the eight usual in macrosemiids. Young specimens of *N. pentlandi* also have fewer than eight lower rays so the low number in *N. ferreri* may again be due to immaturity.

DESCRIPTION. See Wenz (1964).

Family **UARBRYICHTHYIDAE** nov.

DIAGNOSIS. Medium to large, deep-bodied halecostome fishes; ganoine on postorbital region of skull roof forming radiating ridges; all sensory canals on skull of small diameter; frontoparietal suture slightly sinuous; nasals plate-like; supratemporal commissural sensory canal borne entirely by paired supratemporals which meet in the midline; fusion between infraorbital and supraorbital sensory canals behind the eye uncertain; sclerotic unossified; single supraorbital; six plate-like infraorbitals bearing ridges of ganoine; dermosphenotic probably fixed onto skull roof; no suborbitals; gape small, the jaw articulation lying below front of orbit; supramaxilla absent; dentary moderately curved, with sensory canal enclosed in tube; preopercular moderately curved, the sensory canal narrow and communicating with the exterior through narrow pores; distal ceratohyal deepening posteriorly only slightly; dorsal fin undivided, caudal fin forked, no epaxial fin-rays; scales rhomboid.

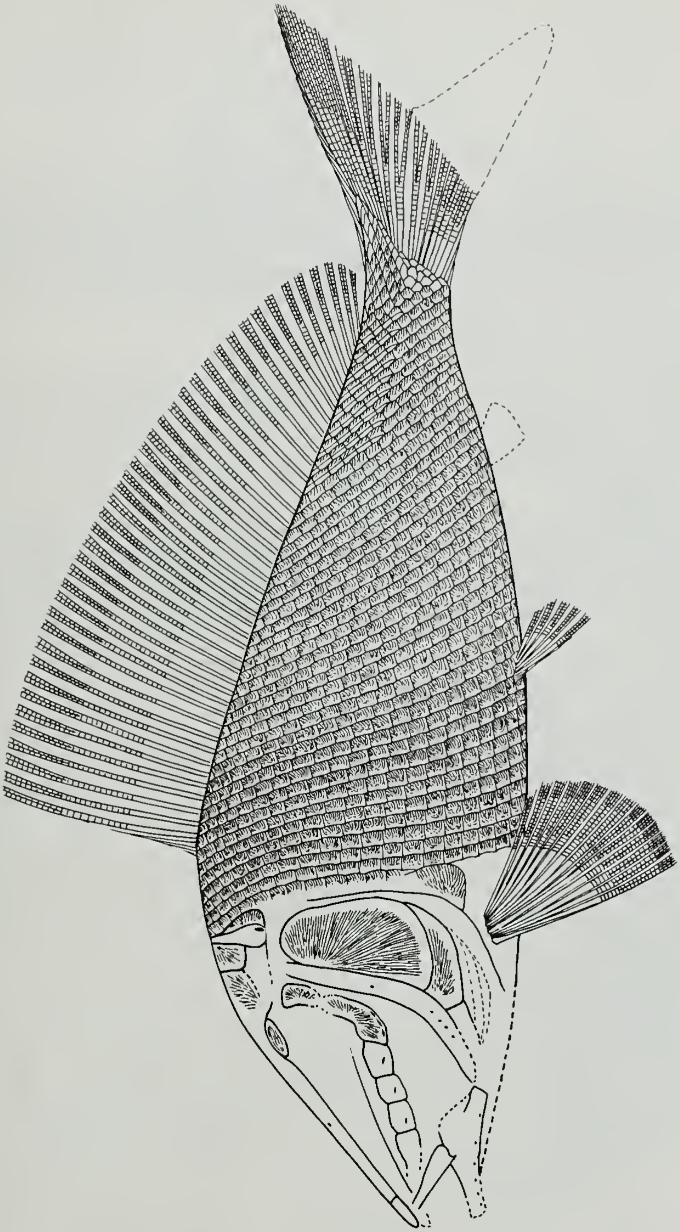

Fig. 44 *Uarbryichthys latus* Wade. Restoration of skeleton. × ½ approx.

RELATIONSHIPS. As explained below, this family is here excluded from the macrosemiids. However, *Uarbryichthys* does share with the macrosemiid *Macrosemius* one specialization unique among actinopterygians. Both genera have secondary transverse scale-rows above the main lateral line, although in *Uarbryichthys* these are confined to the caudal region. It must be presumed that this character arose in parallel in the two genera. On this evidence *Uarbryichthys* is here considered to be more closely related to the macrosemiids than to any other group, since it is not known to share unique specializations with any other holosteans. (The Cretaceous holostean *Aphanepygus* also has secondary transverse scale-rows (Bartram 1977), but these seem to be of a different type.)

Genus *UARBRYICHTHYS* Wade 1941

DIAGNOSIS. Uarbryichthyid reaching standard length of 260 mm; pectoral fin with about 15 rays, no fringing fulcra; dorsal fin with about 40 rays; caudal fin with 18 rays, fringing fulcra on dorsal edge only, long axial lobe covered by about six scale-rows; rhomboid scales ornamented with rugae of ganoine, hind edges smooth, secondary scale-rows intervening between transverse scale-rows above main lateral line in caudal region.

TYPE SPECIES. *Uarbryichthys latus* Wade 1941, the only species.

INTRODUCTION. The genus *Uarbryichthys* was erected by Wade (1941) to include a single species, *U. latus*, from the Jurassic fresh water deposits of New South Wales. Later Wade (1953) described this form more fully, together with another species from the same locality, *U. incertus*. He provides in his account no justification for this separation of species, and to judge from casts of the two specimens they are conspecific.

REMARKS. *Uarbryichthys* was placed within the Macrosemiidae by Wade (1953) on the basis of resemblances with *Ophiopsis* and especially *Histionotus*. But *Uarbryichthys* has neither of the two specializations which are unique to the macrosemiids, the nine infraorbitals and the interopercular remote from the mandible. It is thus excluded from the family here, and placed in a new family, the Uarbryichthyidae.

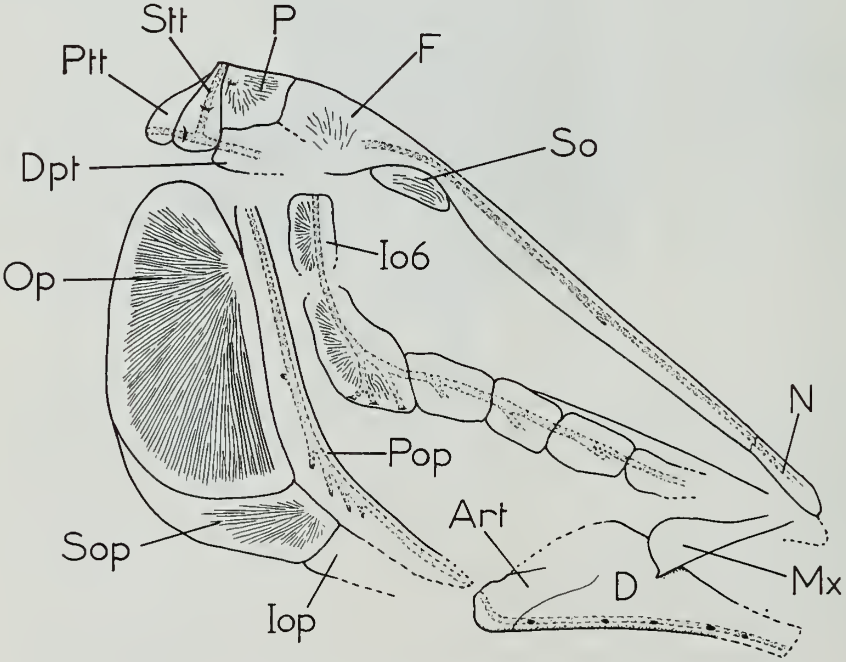

Fig. 45 *Uarbryichthys latus* Wade. Restoration of skull. × ½ approx.

Uarbryichthys latus Wade 1941

Figs 44, 45

1941 *Uarbryichthys latus* Wade : 82.
1953 *Uarbryichthys latus* Wade : 63, text-figs 1, 2; pl. 8.
1953 *Uarbryichthys incertus* Wade : 71; pl. 9.

DIAGNOSIS. As for genus.

HOLOTYPE. Australian Museum, Sydney, F43258a, b.

HORIZON AND LOCALITY. Jurassic of Talbragar, New South Wales, Australia.

MATERIAL. AM: F43258a, b, F43606.

REMARKS. The two known specimens of *Uarbryichthys* are preserved in impression in fine-grained chert. These enabled Wade to give a fairly complete description of the squamation, fins and of the dermal bones of the head. The specimens have been re-examined by means of rubber casts, now in the British Museum (Natural History), and Wade's description checked; it seems to be as good as the preservation of the material will allow.

Infraclass **CHONDROSTEI**

Order ***incertae sedis***

Genus ***TANAOCROSSUS*** Schaeffer 1967

? ***Tanaocrossus maeseni*** (Saint-Seine 1962)

1962 *Macrosemius maeseni* Saint-Seine in Saint-Seine & Casier : 8; pl. 2, figs 1, 2.

DIAGNOSIS. ? *Tanaocrossus* with dorsal part of body above notochord devoid of scales.

HOLOTYPE. Musée Royale de l'Afrique Centrale, Tervuren, 8304.

HORIZON AND LOCALITY. Kimmeridgian of Songa, Zaïre.

REMARKS. Saint-Seine's description of this fish is based upon a single, poorly preserved specimen. He placed it in the genus *Macrosemius* on account of the elongated dorsal fin, which extends from the skull to the caudal fin, and of the large area on either side of the dorsal fin devoid of scales. The bones of the skull, however, are crushed beyond confident recognition and Saint-Seine (in Saint-Seine & Casier 1962 : 9) states that his reconstruction of the head is 'en grande partie hypothétique'.

The first character which suggests relationship to *Macrosemius*, the long dorsal fin, is found in diverse actinopterygian groups and is of little use as an indicator of relationship, as discussed below. The dorsal scale-free area, however, is found elsewhere only in *Macrosemius* and *Legnonotus*, and is stronger evidence of relationship.

There are other features of Saint-Seine's fish which render this relationship unlikely, however. For instance between successive neural spines are two or three short slender bones. Saint-Seine identified these as axonosts (proximal dorsal fin radials), and the rods beneath the dorsal fin-rays as baseosts (middle segments of the radials). This identification is probably correct, as the two elements correspond closely in number; the lower series cannot consist of supraneurals since these occur well in excess of the number of neural spines. The possession of elongate baseosts appears to be a primitive feature which occurs in chondrosteans (*Pteronisculus*, *Birgeria*, *Tarassius*, *Bobasatrania*). In contrast the baseosts of *Macrosemius* and other Neopterygii are short and stout. Also in contrast to *Macrosemius*, Saint-Seine's specimen displays non-branching fin-rays, an unusual feature which rarely occurs in fish other than chondrosteans.

One holostean feature is present, however. The dorsal fin-rays show a one-to-one relationship with their radials. But this feature is also found in the chondrostean Haplolepidae and Perleididae.

Of the known Chondrostei, *Tanaocrossus kalliokoskii* Schaeffer (1967 : 316; pl. 20) from the Upper Trias of Colorado resembles Saint-Seine's fish most closely. They share a similar number (about 75) of non-bifurcating dorsal rays and of caudal fin-rays (about 15). The shape of the body and of the known fins are also very similar. Only the rear part of the skull is known in *T.*

kalliokoskii; the form of the opercular and of the plate-like preopercular bones are taken by Schaeffer (1967 : 316) to indicate chondrostean affinities. The squamation of this species is, however, entire.

Although the similarities between *M. maeseni* and *T. kalliokoskii* are few, the features they share in fin form and ray number are rare among the chondrosteans, to which both fishes seem to belong. For this reason, *Macrosemius maeseni* is here provisionally transferred to *Tanaocrossus*. A brief and inconclusive discussion of the relationships of *Tanaocrossus* is given by Schaeffer (1967 : 317).

The Macrosemiidae in comparison with other Actinopterygians

It will be argued in the succeeding section that the seven genera described above constitute a monophyletic group. In this section their structure is reviewed and compared with that of other actinopterygians. The features which they share with other groups are assessed in the light of the partially cladistic classification of Patterson (1973), in preparation for the discussion of the relationships of the macrosemiids.

(i) Skull roof and braincase. In all macrosemiids (but not in *Uarbryichthys*) the supratemporal commissural sensory canal is enclosed in part by the parietal (possibly a compound parieto-supratemporal, as discussed on p. 143). Many teleosts (e.g. Notopteridae, Osteoglossoidei, Characidae, Gymnotidae) also display this condition (McDowell 1973 : 12).

The sensory canals on the skulls of macrosemiids are remarkable for their large diameters. In groups below the teleost level the canals are housed in tubes of narrow bore and communicate with the surface through fine pores; in most macrosemiids the canals are exposed by large fenestrae. This character was presumably derived independently within the family, since the sensory canals on the skull roof of *Notagogus*, and on the entire skull of *Uarbryichthys*, are enclosed in narrow tubes. The functional significance of large sensory canals in the macrosemiids is unclear; they presumably conferred a high sensitivity on the enclosed sensory organ (Marshall 1971 : 55). Such wide canals are found among teleosts in bathypelagic forms (macrourids, halosaurs).

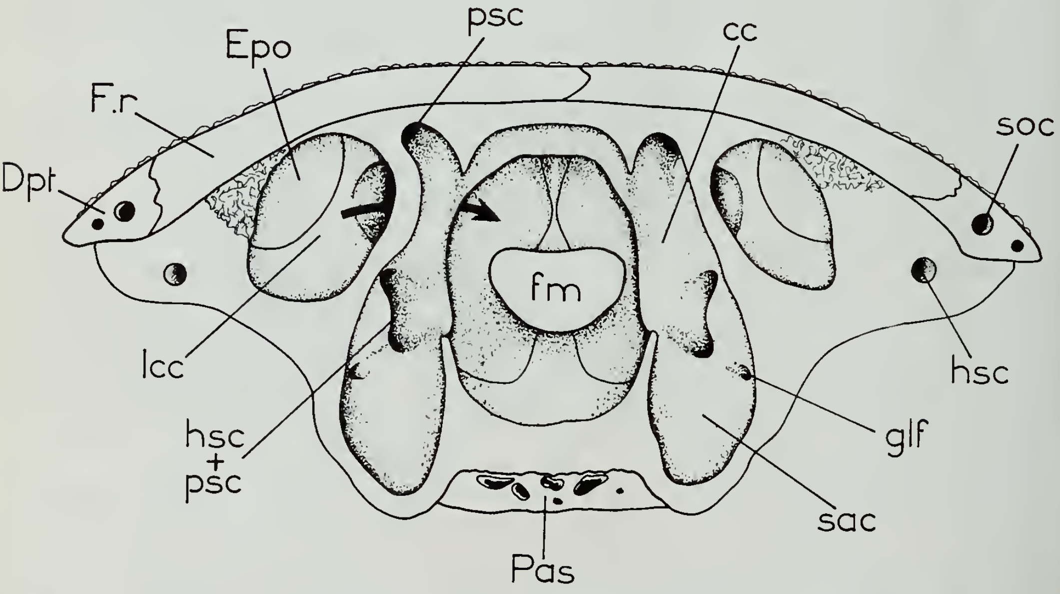

Fig. 46 *Lepisosteus osseus* (Linnaeus). Skull roof and braincase cut transversely through the otic region and viewed from in front to show the lateral cranial canal (arrowed). × 3.

Unfortunately the macrosemiid braincase is known only in medial view in a single specimen of *M. rostratus* (Fig. 3, p. 144). Apart from the occipital fissure, the postorbital chondrocranial ossifications of palaeoniscids fuse together in the adult and give no indication of the primitive actinopterygian ossification pattern. Among neopterygians the occipital fissure occurs only in parasemionotids, pholidophorids (Patterson 1975) and pachycormids (Lehman 1949). In other groups the fissure is obliterated, sometimes by the expansion of the surrounding bones. This has occurred in *Macrosemius*, in which the exoccipital has grown forward and enclosed the vagal canal, as in *Lepidotes* (Rayner 1948). According to Patterson, closure of the fissure has occurred independently in several groups, making this specialization a weak indicator of relationships.

Several braincase bones exhibit a variable occurrence among neopterygians; these are the opisthotic, pterotic, intercalar and supraoccipital. Patterson considers that the first three, and possibly also the last, occurred primitively in actinopterygians. The opisthotic is missing in *Macrosemius*, in which the exoccipital and prootic meet. Among teleosts the opisthotic is absent in all living groups and some pholidophorids, and in halecomorphs it is known to be lost in *Amia* and one species of *Caturus* (*C. furcatus*, Patterson 1975 : 441). It is also lost in *Lepisosteus* and *Lepidotes* (Patterson 1975). The pterotic is present in *Macrosemius* immediately beneath the skull roof, the primitive position of the bone, according to Patterson, as found in caturids, parasemionotids, *Pachycormus*, and probably also *Dapedium*. Again according to Patterson, the intercalar was primitively an endochondral ossification, as retained in parasemionotids and *Pachycormus*. This bone is lost in *Lepisosteus* and *Lepidotes*. A membranous component of the intercalar evolved independently in halecomorphs and teleosts; in *Amia* and living teleosts the endochondral part is lost. In the specimen of *Macrosemius* mentioned above, the inner view of the skull reveals no endochondral intercalar, and of course the membranous component would not be visible in this view even if present. There exists one specimen (Mü AS.I.770) which would probably indicate whether a membranous intercalar is present or not, but it was not available for development in acetic acid. Finally, the supraoccipital is certainly present only in pholidophorids and teleosts (Patterson 1975). It is unknown in *Macrosemius*.

The basisphenoid is not preserved in the specimen of *Macrosemius* displaying the braincase, and may have been absent; as described above, its position is partly occupied by a short, stout pedicel arising from the parasphenoid which divides the entry of the myodome into two. As mentioned above, a similar though smaller process has been found in a palaeoniscid (*Kansasia*) and in pholidophorids and leptolepids. A feature unique to the teleosts, the extension of the posterior myodome beneath the basioccipital, does not occur in macrosemiids as far as is known.

What little is known of the macrosemiid braincase, therefore, gives no evidence of relationship with either the halecomorphs or teleosts.

(ii) Circumorbital series. With the exception of the dermosphenotic, the infraorbital series of *Macrosemius*, *Histionotus* and *Propterus* (the only macrosemiid genera in which the series is known) is remarkably uniform in shape and number. All possess a long tapering antorbital, seven scroll-like infraorbitals below the eye and two tubular infraorbitals behind the eye. There are no suborbitals.

In *Macrosemius*, *Histionotus* and *Propterus* the dermosphenotic forms a short, vertical, perforated tube around the upper part of the infraorbital sensory canal; it resembles the last two infraorbitals, although it appears to have been attached to the skull roof. As in most recent teleosts (Gosline 1965 : 188) the bone does not enclose the junction between the infraorbital and supraorbital sensory canals. In *Notagogus*, in contrast, the dermosphenotic encloses this junction and is fully incorporated into the skull roof. The relationship of the dermosphenotic to the skull roof in various groups has been discussed by Patterson (1973 : 244). In palaeoniscids, pycnodonts and halecomorphs the dermosphenotic is fully incorporated into the skull roof. Elsewhere, the bone is either hinged to the roof, as in *Lepisosteus*, or overlies the sphenotic forming a loose attachment, as in teleosts. Patterson suggests that the former pattern may be primitive, and that the infraorbital-like dermosphenotic of *Lepisosteus* and teleosts is specialized. If this is the case then *Notagogus* displays the primitive macrosemiid condition. In fact the difference between the two types of dermosphenotic may not be profound. The state of the bone is known to change during the development of *Amia*. It originates as a vertical tube around the upper part of the sensory canal, and closely resembles the infraorbitals (Pehrson 1940). Later in ontogeny the bone develops membranous outgrowths and becomes part of the skull roof. If this mode of development was widespread among actinopterygians then the acquisition of an infraorbital-like dermosphenotic within the Macrosemiidae and other groups may have involved a relatively simple process of growth retardation.

The infraorbitals of macrosemiids resemble those of many teleosts. It is generally accepted that the canal-bearing bones of fishes involve two components (Kapoor 1970 : 86). The laterosensory component forms a tube around the sensory canal, from which the laminar component extends. In teleosts the membranous laminar component develops first, and the laterosensory component forms later in association with an invaginating neuromast organ. The two components may be fused from the beginning (*Phoxinus*, *Alburnus*), or may fuse later (*Leuciscus*, *Ophicephalus*) or may remain separate (*Nemacheilus*). In some cases the laterosensory component alone develops. Thus of the five infraorbitals present in mormyrids (Taverne 1971), for example, the posterior three form tubes around the sensory canal; the other two are scroll-like, incompletely surrounding the canal. A similar process seems to have occurred in the Macrosemiidae, in which the antorbital and last two infraorbitals consist of the laterosensory component only. The remaining infraorbitals, forming open gutters around the sensory canal, may comprise a small membranous component in addition.

Patterson (1973) notes that the suborbitals are lost within the Amiidae and within the pholidophorid–teleost group. Although this loss occurred independently within the two groups, he suggests that it may nevertheless indicate relationship between them since this feature is rare elsewhere. It is also found in the Pycnodontidae (Lehman 1966 : 177, *Macromesodon*) and in the chondrostean *Errolichthys* (Nielsen 1955), as well as in the macrosemiids.

It seems that many features of the macrosemiid skull (the scroll-like nasals and infraorbitals, the trough-like preorbital region of the frontals, the absence of suborbitals and the form of the dermosphenotic) are manifestations of a trend involving the general reduction of laminar dermal bone. These features are emphasized by the large size of the sensory canals. In *Uarbryichthys* none of the bones form troughs or scrolls; the sensory canals are housed in narrow tubes. Suborbitals are absent in this genus too, however.

(iii) Hyopalatine bones. The ossifications in the palate of macrosemiids conform to the usual neopterygian pattern, such as that of *Amia*. The presence of two dermopalatines (known in *Macrosemius*) is probably a primitive feature as Patterson (1973 : 246) suggests; it is found in the chondrosteans *Pteronisculus* (Nielsen 1942), *Elonichthys* (Watson 1925) and in some individuals

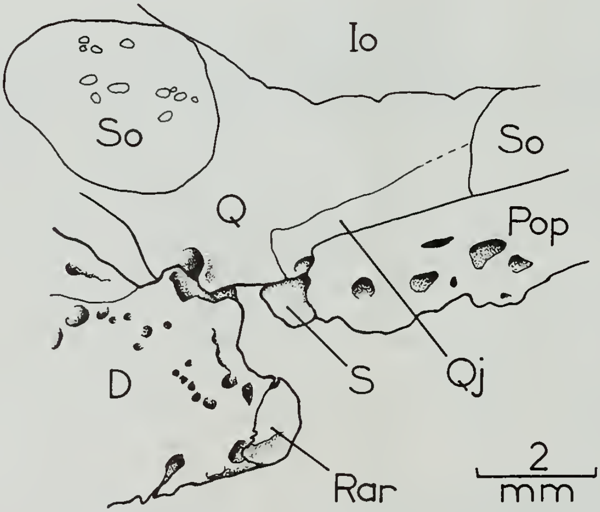

Fig. 47 *Furo longiserratus* (Agassiz). Region of left jaw articulation of CM 5021.

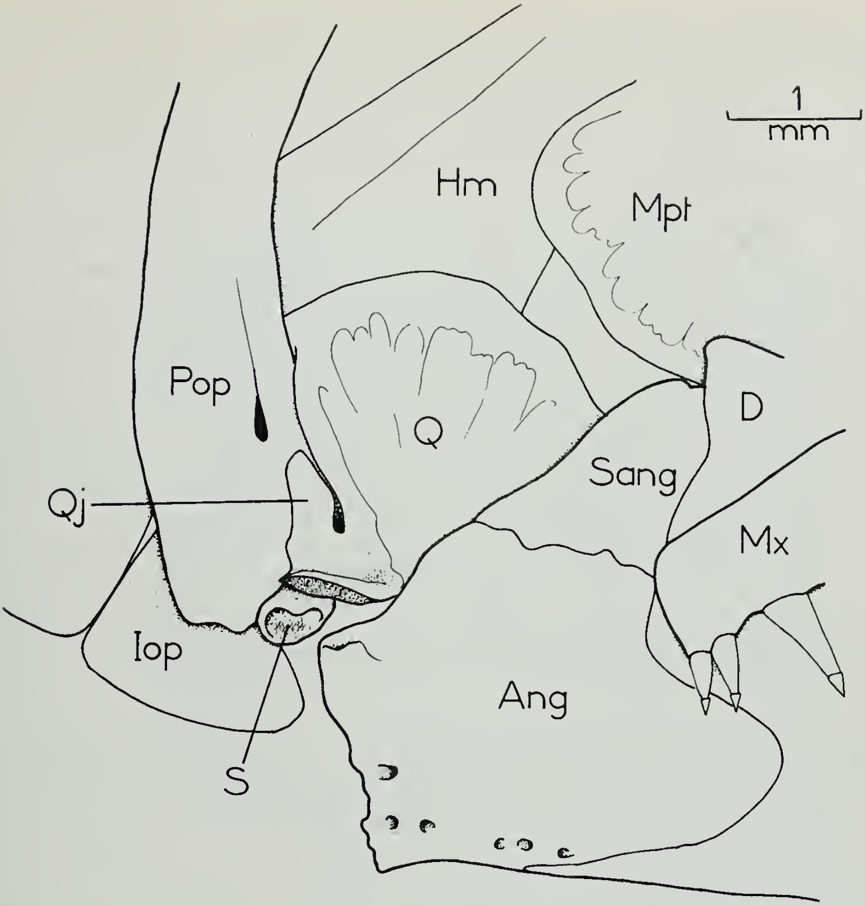

Fig. 48 *Caturus* sp. from the Lower Kimmeridgian of Bavaria, P44900. Region of right jaw articulation.

of *Ospia* (Stensiö 1932 : 252), as well as in *Amia*. The palate of macrosemiids usually ossifies fully, although a gap may persist between the metapterygoid and quadrate.

The neopterygian quadrate is associated with a separate ossification of the hyomandibular cartilage, the symplectic, and with a dermal bone, the quadratojugal. Patterson (1973) has discussed at length the relationships between these three elements.

Three patterns may be recognized. In *Lepisosteus*, *Lepidotes* and *Dapedium* (Patterson 1973 : figs 6, 26) the quadratojugal is an elongated bone lying along the upper edge of the ventral arm of the preopercular; the anterior end of the bone abuts against the articular condyle of the quadrate. No fusion occurs between the quadratojugal and quadrate in *Lepisosteus* and in Patterson's specimens of *Lepidotes* and *Dapedium*. In none of these forms does the symplectic come into contact with the mandible. In *Lepisosteus* the symplectic is small and remote from the quadrate; in *Lepidotes* and *Semionotus* it forms a long rod lying medial to the quadrate and quadratojugal.

The second pattern is found in living teleosts and their fossil relatives. The quadratojugal is probably represented by the spine-like posterior process of the quadrate, as held by Holmgren & Stensiö (1936 : 463). This condition is advanced relative to that of *Lepisosteus*, in which the quadratojugal remains discrete. The symplectic of teleosts is typically a long tapering bone which is inserted into a groove formed between the quadrate and its posterior process on their inner surface; thus in these fish too no contact between the symplectic and the lower jaw occurs.

The third group comprises the Parasemionotidae, Caturidae and *Amia*. In these forms the quadratojugal is absent (*Amia*) or reduced to a small flange of bone on the quadrate as in parasemionotids (Patterson 1973 : fig. 23), *Furo* (fig. 20) and *Caturus* (Fig. 48). Patterson suggests that this reduction of the quadratojugal is a derived character; it probably is, but it must have been acquired several times in these groups, since a large, discrete quadratojugal is present in *Furo longiserratus* (Fig. 47), in specimens CM 5021a and BM(NH) 37081. The symplectic of *Amia* is unique among living holosteans and teleosts in forming an articulation with the lower jaw, posterior to that of the quadrate (Allis 1897: pl. 20). Such an articulation also occurs in the parasemionotids and caturids (Patterson 1973 : figs 20, 23). With some hesitancy Patterson holds that the symplectic jaw articulation is a major specialization acquired independently by these fishes, indicating that they form a monophyletic group, the Halecomorphi.

The quadratojugal in the Macrosemiidae is a long stout bone lying along the entire length of the ventral arm of the preopercular. The expanded anterior end of the bone fits tightly behind the thin lateral part of the large articulatory condyle of the quadrate. In *Macrosemius* and perhaps also in *Histionotus* and *Notagogus*, fusion occurs between these two bones in this region; the quadratojugal of *Propterus* remains free. In teleosts the quadrate and quadratojugal are fused from the beginning or fuse early in ontogeny, and Patterson considers this to be a teleost specialization. In macrosemiids, in contrast, if fusion occurs at all, the two bones fuse late in development. This is probably also true of the 'semionotids' (Patterson, pers. comm.).

The macrosemiid symplectic is known only from one specimen of *Propterus elongatus*, although the identification of this bone is not certain, as discussed on pp. 172–3. Whatever the form of the symplectic in this family, there is no evidence to suggest that it formed an articulation with the lower jaw. Only one articulatory facet occurs on the mandible, and this is fully occupied by the broad quadrate condyle. For this reason it is unlikely, in the present state of knowledge, that the Macrosemiidae are halecomorphs.

The hyomandibular of *Macrosemius*, *Propterus* and *Histionotus* displays a specialization in the form of a long flange on the outer surface, alongside the leading edge of the preopercular. Osse (1969 : 383, fig. 24a) has discussed the function of a similar flange in *Perca*, in which it serves for the origin of the upper part of the adductor mandibulae muscle. This narrow zone of origin for the muscle leaves the lateral surface of the hyomandibular anterior to the flange free for the insertion of the long levator arcus palatini muscle. The latter is unusually long, its length presumably compensating for the restricted area available for its origin on the short postorbital region of the skull. Since the postorbital region is also short in the macrosemiids, the flange on the hyomandibular may have arisen to meet similar functional demands, that is, to allow for the presence of an elongated levator arcus palatini muscle.

(iv) Dermal upper jaw. The supramaxilla is lacking in the Macrosemiidae; the absence of this bone is very rare among fish with a free, mobile maxilla. It is absent in the pycnodonts, *Besania*, *Luganoia* (Brough 1939 : figs 15, 20) and in *Acentrophorus* (Gill 1923). There is a single supramaxilla in the remaining 'semionotids' and in the Halecomorphi, and two in the pholidophorids and primitive living teleosts. In *Elops* (Vrba 1968 : 228, fig. 3), the posterior ends of the supramaxillae are fixed to the maxilla; when the jaws open, 'the supramaxillae fold out as from a fan, providing some firmness to the unprotected lateral wall of the mouth'. This function was presumably primitive for holosteans and teleosts, since there seems to be no other explanation to account for the evolution of the supramaxilla in these fishes. In *Amia calva*, however, the supramaxilla is firmly fixed to the maxilla and clearly in certain other groups, for example the pachycormids (Wenz 1968 : figs 52, 67), the bone was also incapable of performing the function described in *Elops*.

The absence of the supramaxilla in the forms listed above is associated with the possession of short jaws, where the area of the walls of the open mouth is small and thus may have needed less support than in long-jawed forms. In *Macrosemius* and *Propterus* such support may have been provided by the ventral extensions of the anterior three infraorbitals. There are no means of knowing, on present evidence, whether the absence of the bone in macrosemiids is a primitive halecostome feature, or whether it is due to secondary loss. The bone is also absent in *Uarbryichthys*.

The number and form of the maxillary teeth in the macrosemiids varies. A long row of maxillary teeth occurs in *Legnonotus* and *Notagogus*; these genera probably took small prey. In *Macrosemius* and *Propterus* the maxillary teeth are reduced in size and number, and restricted to the posterior part of the maxilla; in *Histionotus* they are absent. In *Macrosemius* at least, the vomers, palatines and splenials bear a crushing dentition. The coincidence of a reduction or absence of maxillary teeth and the possession of a crushing dentition occurs in the pycnodonts and in some 'semionotids', for example *Dapedium politum* (Wenz 1968) and *Acentrophorus varians* (Gardiner 1960).

The macrosemiid premaxilla forms a stout 'ascending process', renamed the nasal process by Patterson (1973). The process passes beneath the nasal and forms a suture with the dorsal ethmoid ossification. The nasal process is known also in *Lepisosteus*, *Amia*, caturids, 'semionotids', parasemionotids and *Perleidus* (Patterson 1975), and appears to be a primitive feature of the Neopterygii. The nasal process of *Amia* develops as a separate ossification, the rhinal bone of Bjerring (1972 : 193), and Patterson (1975 : 512) has shown that in teleosts and their fossil relatives the process separates from the dentigerous part of the premaxilla, forming 'dermethmoids'. In living teleosts these may fuse with the rostral or become incorporated into the mesethmoid.

The nasal process of *Lepisosteus*, *Amia*, *Lepidotes* and *Semionotus* completely surrounds the olfactory nerve and lines the nasal pit. In macrosemiids, however, the process passed lateral to the nerve and did not enclose it. A similar relationship between the olfactory nerve and nasal process occurs in *Ophiopsis* (Bartram 1975), *Furo latimanus* (personal observation), *Dapedium*, *Acentrophorus*, parasemionotids (Patterson, 1975: figs 134, 136, 137), and possibly also in *Luganoia* (Brough 1939: 46).

(v) Lower jaw. Macrosemiids possess the following dermal elements in the mandible, in common with *Amia*, *Lepisosteus* and *Pholidophorus* (Patterson 1973 : fig. 7): dentary, angular, surangular, prearticular and coronoids (one in *Macrosemius*).

The Meckelian cartilage in macrosemiids forms two ossifications. The larger forms the broad, rearward-facing facet for the quadrate, and the tall coronoid process. The second ossification is the retroarticular. Among living forms this bone occurs in *Lepisosteus*, *Amia* (ossicle 'a' of Bridge, Allis 1897 : pl. 20) and in the teleosts (angular of Goodrich (1930), Gosline (1969)). Nelson (1973 : 179) has considered the relationship between the retroarticular and the facet for the jaw articulation. Referring to extant forms he notes that in *Latimeria*, *Lepisosteus*, *Amia* and in some osteoglossomorph (*Arapaima*, *Heterotis*) and elopomorph teleosts, the retroarticular forms part of this facet. He considers this to be the primitive condition; in most teleosts the retroarticular is excluded from the joint. However, the retroarticular also appears to be excluded from the joint in some non-teleost fossils (*Macrosemius*).

(vi) Preopercular, hyoid arch and opercular series. These elements display several features of special interest in the macrosemiids: the small size of the interopercular, the form of the branchiostegal rays and the absence of a gular.

The upper branchiostegal rays of macrosemiids are acinaciform; that is to say they form curved, overlapping, non-laminar blades. Acinaciform branchiostegals, of a different type, have previously been known only in the higher teleosts (McAllister 1968 : table 1). The branchiostegal rays of most chondrosteans and holosteans are spathiform, forming laminar, scarcely overlapping plates, as in the palaeoniscids (Nielsen 1942), parasemionotids (Lehman 1952), pachycormids (Lehman 1949), *Amia* (Jessen 1968) and *Caturus* (Fig. 50). The hyohyoideus muscle in these fossil groups presumably formed a continuous sheet over the inner side of the branchiostegal rays, as in *Amia*, *Salmo*, *Clupea*, *Albula* and *Esox* (Edgeworth 1935 : 101). This muscle probably performed the function ascribed to it by Vrba (1968 : 227) in *Elops*, in which it contracts during inspiration, holding the branchiostegal membrane against the sternohyoideus musculature and preventing the inflow of water into the opercular cavity. This is undoubtedly the primitive function of the muscle.

In higher teleosts, however, an active branchiostegal pump occurs which supplements the action of the operculum in lowering the pressure in the opercular cavity (Baglioni 1907). In such fish, the branchiostegal rays are highly movable, and are spread and collapsed like a fan by the action of the modified hyohyoideus muscle. Thus in *Perca* (Osse 1969 : 335, fig. 12), the hyohyoideus muscle differentiates into a superior portion which passes from ray to ray, and an inferior part which connects each ray to the ceratohyal. Contraction of the hyohyoideus inferior thus expands the branchiostegal membrane, and the contraction of the hyohyoideus superior collapses the membrane. The form and overlapping of the branchiostegals in macrosemiids suggest that members of this family also possessed a branchiostegal pump mechanism. That this was the case is supported by the fact that most macrosemiid specimens are preserved with the branchiostegal rays widely spread, presumably by the action of a hyohyoideus inferior muscle.

The mandible in chondrosteans was presumably depressed by the action of muscles connecting it with the hyoid arch (Millard 1966 : 37). In holosteans and teleosts, however, another mechanism has arisen involving a new element, the interopercular. With the exception of the pycnodonts, the interopercular is present in all actinopterygians in which the maxilla is movable. Patterson (1973 : 246) can find no evidence to suggest that its absence in *Lepisosteus* is due to loss, and considers this absence to be a primitive feature shared with the Chondrostei.

In *Amia* (Allis 1897 : pl. 20) ligaments extend from the retroarticular in the mandible to the interopercular, to the uppermost branchiostegal ray and to the proximal ceratohyal, and from the latter bone to the interopercular. A similar set of couplings occurs in living teleosts (*Elops*, *Albula*, *Clupea*, *Salmo* – Gosline 1969 : 192). The lowering of the mandible by the pull of these ligaments may be brought about in various ways. Thus contraction of the levator operculi muscle would cause backward movement of the interopercular and of the ceratohyal, to which it is connected, or a similar movement of these two bones may be caused by contraction of the sternohyoideus muscle.

In *Lepisosteus*, in which the interopercular is absent, a long, thick ligament extends from the retroarticular to the proximal ceratohyal (personal observation; this contradicts Gregory's (1933 : 127) observation that this ligament ran to the quadratojugal, which he called the interopercular). If Patterson is correct in considering the absence of an interopercular in this fish a primitive feature, and *Lepisosteus* the most primitive known neopterygian, then the presence of a hyoideomandibular ligament and an indirect method of opening the jaws in this fish is surprising, since it suggests that they arose before the appearance of the interopercular. The view that this ligament is the more primitive is held by Gosline (1969 : 192), who points out it is very large in *Amia*, in which the interopercular has little to do with the opening of the mouth. Following her work on *Elops*, Vrba (1968 : 232) arrives at the same conclusion.

But the fossil evidence, in contrast, seems to indicate that the interopercular was involved in the opening of the mouth from an early stage in the evolution of the halecostomes, and indeed arose in association with this function. Thus in fossil forms in which the jaw articulation has shifted forward (*Lepidotes*, *Semionotus*, *Dapedium*, *Pholidophorus*, *Lycoptera*) the interopercular is very long and maintains a close proximity to the hind end of the mandible. This correlation also occurs in teleosts with forwardly-placed jaws, for example *Chanos* and the cyprinoids. In the perch (Osse 1969 : 337, 359) the mandible is depressed by the contraction of the levator operculi muscle acting *via* the interoperculomandibular ligament.

In view of these facts, the remoteness of the interopercular from the mandible in macrosemiids is surprising. The significance of this feature is not clear; whichever tendons inserted upon the retroarticular must have been very long. There is some evidence to indicate that the uppermost branchiostegal ray was modified, serving for the origin of a tendon which inserted upon the lower jaw, as in *Amia*. The proximal ends of the lowermost seven rays are expanded and articulated with the lateral surface of the ceratohyal; in contrast, the uppermost ray tapers proximally forming no such expansion, and its blade was overlapped by, and probably fixed to, the subopercular.

The gular plate has been lost in most living actinopterygians. The median gular is retained in *Amia*, Elopidae, Megalopidae, *Albula* (Nybelin 1960) and *Luciocephalus* (Liem 1967 : 118). Among fossil holosteans the gular is known to be lost only in *Lepidotes*, pycnodonts, aspidorhynchids and macrosemiids. In all living forms with a gular, this bone is connected to the mandibular rami by a division of the intermandibular muscle. and to the ceratohyals by the interhyoideus muscles (Liem 1967 : 118). During respiration and feeding, the anterior ends of the ceratohyals are pulled downwards by the action of the sternohyoideus muscles, depressing the gular and hence the floor of the mouth. Thus the gular serves to spread over a large area of the floor of the mouth what would otherwise be a local effect. The loss of the gular in the Macrosemiidae and in most teleosts may be associated with the forward position of the jaw articulation. Gosline (1967 : 238) has noted the correlation between the latter feature and the presence of a short ceratohyal. Such a ceratohyal, with its anterior end at the level of the quadrate condyle as in macrosemiids, is in no position to depress a gular plate, unless this were very large; this may partly account for the loss of the bone.

(vii) Vertebral column. Monospondylic ring centra are present in the abdominal region of *Macrosemius*, *Histionotus* and *Enchelyolepis*. These centra are thick, constrict the notochord and fuse with the arches; their greater part was composed of perichordal, endochondral bone. Although the anterior vertebrae of *Notagogus* also form rings, these separate into dorsal and ventral crescents in the caudal region. Whether they are mainly chordacentral or not is difficult to assess. In *Propterus elongatus*, centra are formed only in the first few segments; they consist of dorsal crescents alone, and are probably chordacentral.

The Neopterygii present a rich diversity of central ossification patterns in both origin (chorda- or autocentral) and form (rings, solid cylinders or crescents). Thus thin ring-like chordacentra are present in the teleosts *Ichthyokentema* (Griffith & Patterson 1963 : 26, fig. 12), *Catervariolus* (Saint-Seine 1955 : fig. 47) and *Euthynotus* (Wenz 1968); such centra have not been recorded in halecomorphs. Thick centra, composed mainly of endochondral bone and constricting the notochord like those of *Macrosemius*, are found in the Caturidae. They may form crescents, as in some species of *Furo*, *Caturus* and *Osteorachis* (Patterson 1973 : 281) or thick annuli, as *F. microlepidotus*, *Neorhombolepis* (Woodward 1918 : 87), *Macrepistius* (Schaeffer 1960 : fig. 5) and *Ophiopsis* (Bartram 1975). In the last genus, the presence of dorsal and ventral hemichordacentral components has been demonstrated, and such a chordal contribution to annular centrum formation probably occurred in other caturids.

The neural spines of macrosemiids are known in the abdominal and caudal regions in *Propterus* and *Enchelyolepis*; they are paired. Paired neural spines occur also in chondrosteans and *Lepisosteus*, and this is probably the primitive neopterygian condition (Patterson 1973 : 236). Median neural spines are found in the caudal regions of *Amia* and the teleosts, and Patterson considers

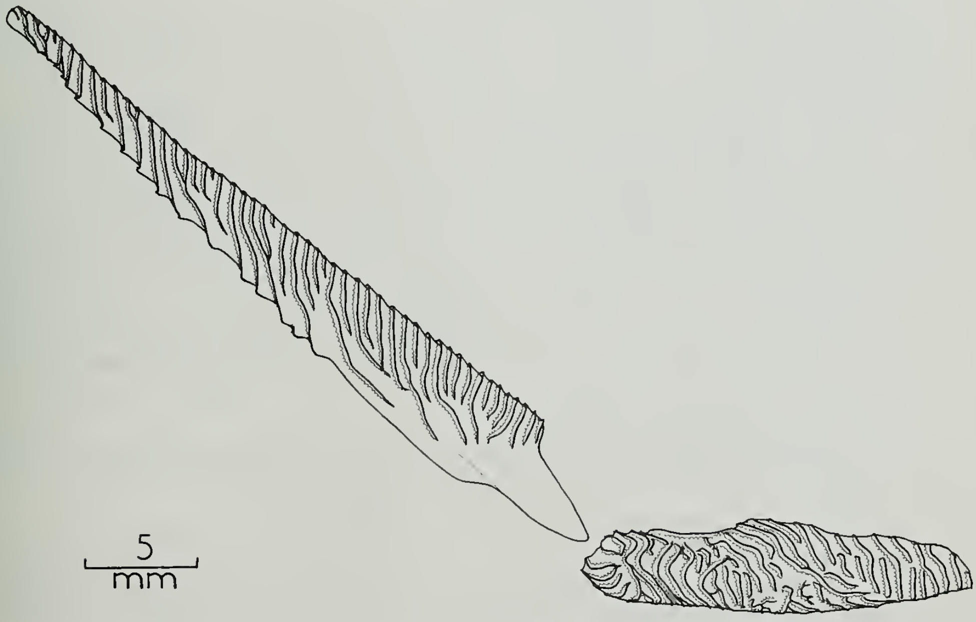

Fig. 49 *Amia calva* Linnaeus. Serrated appendage and denticle-bearing plate of right side.

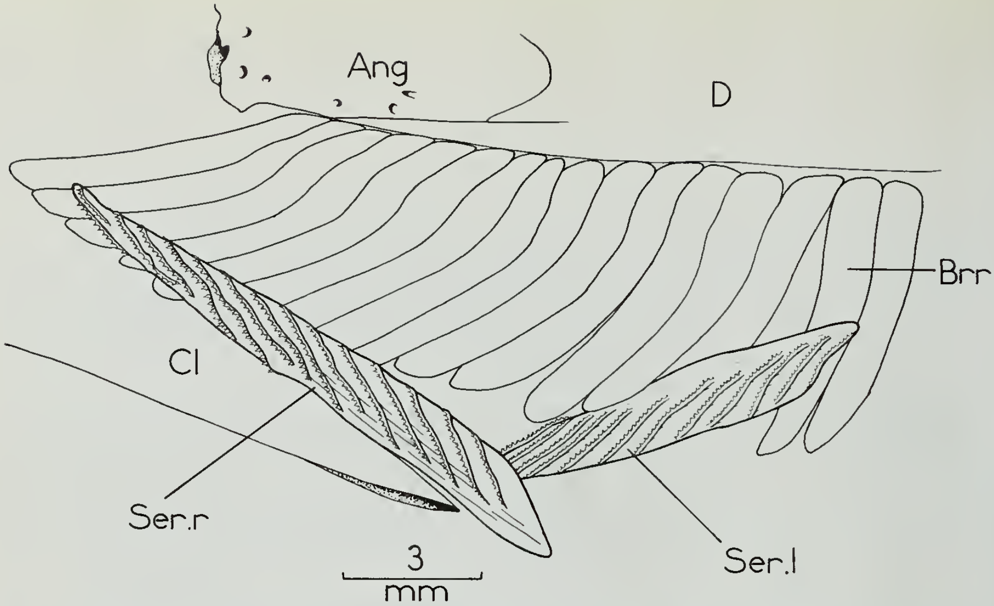

Fig. 50 *Caturus* sp. from the Lower Kimmeridgian of Bavaria, P44900. Left and right serrated appendages, branchiostegals and ventral parts of mandible and cleithrum, as preserved.

this specialization indicative of relationship between these two groups; it also occurs in their fossil relatives. Median neural spines also occur in *Dapedium*, *Tetragonolepis* and pycnodonts (Patterson 1973) and in the palaeoniscoids *Australosomus* and *Birgeria* (Nielsen 1949). The presence of paired neural spines in the Macrosemiidae provides a strong indication that this family belongs neither in the Halecomorphi nor in the Teleostei.

(viii) Pectoral girdle and fin. The discovery of a serrated appendage in one specimen of *Propterus elongatus* is of special interest, since such a bone is known to occur only in *Amia* (Fig. 49; Wilder 1876 : 259) and *Caturus* (Fig. 50). That of *Amia* is discussed by Liem & Woods (1973).

Both left and right serrated appendages are preserved in an acid-prepared specimen (BM(NH) P44900) of *Caturus ?furcatus* of standard length 130 mm. The right appendage, the better preserved, lies along the ventral arm of the cleithrum. Its surface is traversed by 14 ridges bearing small, three-spined denticles pointing posteriorly; similar denticles occur in vertical rows on the cleithrum. As in *Amia*, the ridges slope forward dorsoventrally, although in contrast to *Amia*, the ridges are all of approximately equal length and do not branch. The proximal end of the appendage was presumably embedded in the sternohyoideus musculature, the remainder of the bone projecting freely into the opercular cavity. That the appendage did project, rather than lie embedded in the skin, is indicated by the presence of denticles on the medial surface; these are visible in the specimen at the distal tip of the bone. In addition to the appendage, *Amia* also possesses a flat plate of bone, also bearing denticulated ridges, embedded in the skin covering the sternohyoideus muscle; this is absent in the specimen of *Caturus*.

The serrated appendage of *Propterus* differs from those described above in forming only a single row of denticles along the leading edge. Its curved form suggests that it did indeed project into the opercular cavity.

The homologies of these denticle-bearing plates and appendages are not obvious. The most likely candidate is the clavicle of chondrosteans and crossopterygians (Liem & Woods 1973). In the former, the ventral arm of the cleithrum is very short and preceded by a large clavicle, as in *Acipenser* (Jessen 1972 : fig. 2). The sternohyoideus muscle originates either on the inner surface of the clavicle and cleithrum (*Polypterus*, Jessen 1972 : pl. 16, figs 1, 2), or is continuous with the ventral body musculature (*Acipenser*, Jessen 1972 : pl. 13, fig. 1) and did not attach to the pectoral girdle. In teleosts the clavicles are lost; the sternohyoideus muscle originates on the outer surface of the elongated ventral arm of the cleithrum (*Elops*, Jessen 1972 : pl. 7, fig. 4) or again is continuous with the ventral body musculature (*Salmo*, Jessen 1972 : pl. 15, fig. 1). In *Lepisosteus* and *Amia* the sternohyoideus muscle has a similar area of origin to that of *Elops*. Two or three elongated plates of bone, bearing scattered denticles and patches of ganoine, are embedded in the skin covering this muscle in *Lepisosteus* (Liem & Woods 1973 : pl. 4b); Jarvik (1944) considered these plates homologous with the clavicles of chondrosteans. Since both lie lateral to the sternohyoideus muscles, this seems likely. If the identification is correct, there is no doubt that the serrated plates and appendages of *Amia*, *Caturus* and *Propterus* are derived from the clavicle too. However, in *Lepisosteus*, additional bony plates may occur on the cleithrum (Fig. 51). They are much smaller than the two or three large plates described by Jarvik, which they resemble in bearing denticles and ganoine. The smaller plates lie alongside the larger plates, and in the skin covering the dorsal arm of the cleithrum. Thus bony plates are able to form in the dermis over a large area of the cleithrum and it is by no means clear that this ability is derived from the ability to form the clavicle of chondrosteans.

Whatever the homologies of the serrated appendage in *Propterus*, its presence cannot be taken as evidence of relationship with the amiid–caturid group until the distribution and form of this element is more widely known among the Neopterygii. Although suggestions have been made (Wilder 1876 : 259, Wright 1884, Liem & Woods 1973), the functions of the serrated appendage remain a mystery.

(ix) Dorsal and anal fins. The macrosemiids are remarkable in possessing a long dorsal fin. This feature was probably acquired independently by the family, although elongated dorsal fins occur in other non-teleosts. They are present in amiids (*Amia*), caturids (*Macrepistius*, *Ophiopsis*) and, in association with a deep body, in pycnodonts, platysomid chondrosteans and some

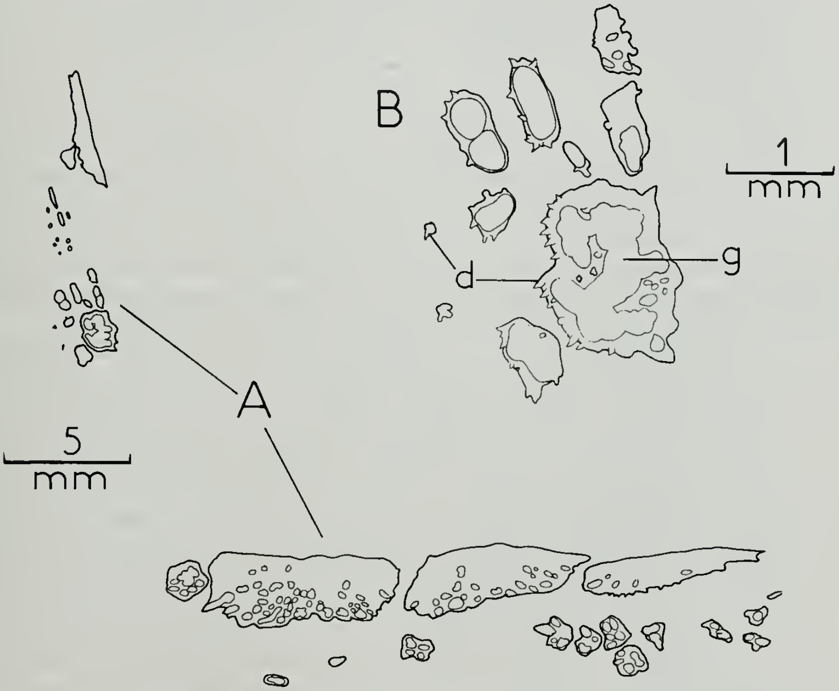

Fig. 51 *Lepisosteus osseus* (Linnaeus). A, denticle-bearing plates in skin over cleithrum of right side. B, upper plates enlarged.

'semi-onotids' (*Dapedium*). *Histionotus, Propterus* and *Notagogus* are the earliest known actinopterygians in which the dorsal fin is divided.

The single dorsal fin of *Macrosemius* resembles that of *Amia calva* and was probably used in a similar way. During rapid locomotion, *Amia* folds down the anterior part of the dorsal fin, the posterior part remaining erect and supplementing the thrust produced by the rounded caudal fin (personal observation). That *Macrosemius* used the dorsal fin in a similar way is suggested by the large, rounded form of the anal fin which presumably balanced the thrust. Slow locomotion in *Amia* is effected by the passage of waves along the dorsal fin while the trunk is held straight; these waves may pass fore or aft. During braking the pectoral fins are held vertically, and their action is supplemented by the dorsal fin, which is thrown into forwardly-passing waves. Harris (1937), and see Patterson's (1964 : 451) discussion, drew attention to the fact that pectoral fins placed low on the body, such as those of *Amia*, would tend to pitch the fish if they were used as brakes. A long dorsal fin may be used to counteract this tendency.

The leading rays of the first dorsal fin in *Propterus* and *Histionotus* are greatly elongated, whereas those following decrease rapidly in height. The leading anal fin-rays of these genera are also long; such fins are unknown in other non-teleosts, and their significance is not clear. Perhaps these fins were capable of erection and depression and served as releaser stimuli to other individuals, for example during territorial or sexual display.

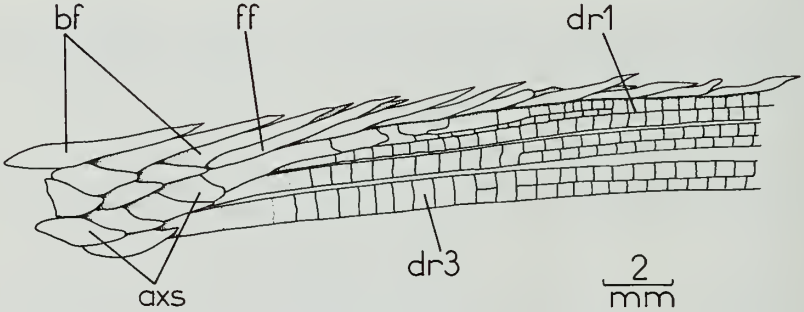

Fig. 52 *Lepisosteus osseus* (Linnaeus). Uppermost fin-rays of caudal fin viewed from the left.

(x) Caudal fin. The caudal fins of macrosemiids are primitive in at least two respects: epaxial fin-rays are absent, and there is no sharp distinction between the uppermost ray and the axial lobe squamation.

Epaxial fin-rays, articulating with epurals and preural neural spines, are a specialization shared by many groups (pholidopleurids, pycnodonts, amiids, teleosts, pachycormids, saurichthyids) but I do not think they are indicative of relationship, as Patterson (1973 : 297) suggests.

Unlike the other axial lobe rays, the uppermost does not insert beneath the squamation proximally, but remains superficial, and is not sharply delimited from the axial lobe scales. A similar phenomenon occurs in *Lepisosteus*, in which the uppermost ray clasps the tip of the notochord (Fig. 52); in contrast, the remaining axial lobe rays penetrate beneath the squamation and clasp the hypurals. Among 'semionotids' the longest axial lobe scale-row continues wholly (*Acentrophorus varians*) or partly (*Dapedium orbis*) along the uppermost ray (Gill 1923 : figs 15, 16). In some pholidophorids too the reduced uppermost ray has remained superficial (Patterson 1968 : fig. 3), and in a species of *Caturus* with cycloid scales (BM(NH) 37095) the uppermost ray does not penetrate beneath the urodermals, unlike its deeply-clasping successors (personal observation). Since the fin-rays were presumably primitively scale-like and superficial, as they are in *Aeduella* (Heyler 1969 : 192), the retention of scale-like characters by the uppermost ray is likely to be a primitive actinopterygian character, and no indicator of relationships.

The caudal fins of macrosemiids are remarkable for the constancy of number of the eight lower, non-axial lobe rays. Variation in caudal fin-ray number occurs only in the axial lobe rays; there are eight of these in *Histionotus*, 7–8 in *Propterus*, 5–6 in *Legnonotus*, 4–6 in *Notagogus* and 3–5 in *Macrosemius*. As in teleosts (Marshall 1971 : 32, Gosline 1969 : 162), a low caudal fin-ray number is associated with weakly-forked or rounded fins. Thus in *Histionotus*, the two lobes of the deeply-forked fin are each supported by eight rays, whereas the single rounded lobe of *Macrosemius* is supported mainly by the eight lower rays. A similar predominance of the lower rays appears to occur in the rounded caudal fin of *Dapedium pholidotus* (Wenz 1968 : fig. 38). Unfortunately too few reliable drawings of the caudal fins of chondrosteans and holosteans have been made; it would be interesting to know the relationship of the caudal fin-rays, the axial lobe and its scales and the termination of the lateral line in various groups.

(xi) Squamation. Schultze (1966) has made a comparative study of the scales of neopterygians. Both *Amia* and living teleosts possess cycloid scales. These are thin, flexible, rounded in outline and deeply overlapping; ganoine and peg-and-socket articulations are absent. Schultze distinguishes between those of *Amia* (Amiiden-Rundschuppe) and those of the teleosts; the surface of the former is raised into radial ridges, and that of the latter into concentric ridges. Although most macrosemiids have rhomboid scales, at least in the adult, both *Enchelyolepis* (Schultze 1966 : fig. 34) and young individuals of ? *Notagogus pentlandi* (Schultze 1966: 276) have cycloid scales with a radiating ornament on the overlapped surface. For several reasons, however, this cannot be taken as evidence of relationship between macrosemiids and halecomorphs.

According to Kerr (1952 : 68), the radiating ridges on the scales of *Amia* are due to the fusion of 'calcified rods'. At the periphery of the overlapped part of the scale 'the rods lie free, losing their calcification and ending as homogenous knobs of collagen immediately below the epidermis'. The periodic bending of the rods is 'the result of a twisting within the substance of the collagen sheet' in which they originate. The fused rods are underlain by a non-mineralized fibrous layer. In a young specimen of *Caturus* sp. (BM(NH) P44900), the overlapped portion of the scale is also formed of fine rods, free from each other along most of their length and exhibiting periodic bending, as in *Amia*. These were stabilized by the underlying fibrous layer which in this specimen had just begun to mineralize. In older specimens of *Caturus* (Schultze 1966 : figs 3a, b, 51) the rods are fused together (forming the 'Knochenschicht'), and the fibrous layer ('Faserschicht') becomes fully calcified. In the primitive teleost *Leptolepis* (Schultze 1966 : fig. 50) the scales when examined in section are seen to be very similar to those of *Caturus*; the main difference between the two lies in the pattern of surface ridges. That there is no fundamental distinction between the two types of cycloid scale is suggested by several facts. Thus Schultze has shown that in several holosteans with rhomboid scales (*Macrosemius*, *Pholidophorus*, pachycormids), the bony layer of the scale beneath the ganoine displays both radial and concentric markings. Further, in the pholidophorid *Pholidophoropsis* (Schultze 1966 : 278) cycloid scales are present with radial ridges. Finally, in the chondrostean genus *Coccolepis*, cycloid scales with both types of marking occur. *C. woodwardi* Waldman displays scales with concentric ridges (Waldman 1971 : pl. 2, fig. 4), or with fine sinuous radii (pl. 2, fig. 5). Waldman writes of the latter: 'on reaching the margin of the scale, the radii protrude over the edge by a minute amount. These protrusions would probably have been embedded in tissue.' This condition is very similar to that which occurs in *Amia* and *Caturus*.

Thus the ability to form cycloid scales of the *Amia*-type is not confined to fossil relatives of this genus, and thus their occurrence in the Macrosemiidae gives no indication of relationship between the two groups. The presence of cycloid scales in young ? *Notagogus* (they are rhomboid in the adult) is a possible indication that such scales are the first to be formed in other actinopterygians with rhomboid scales; thus the appearance of cycloidy in the adults of diverse groups (halecomorphs, teleosts, palaeoniscids such as *Cryphiolepis*, *Disichthys* and *Coccolepis*) may be due to the retention of a juvenile character, rather than to the evolution of a new one.

The squamation of *Macrosemius* displays two features of special interest: secondary scale-rows intervening between the regular transverse rows above the lateral line (found also in *Uarbryichthys*), and a lack of scales in a wide strip on either side of the dorsal fin (occurring in *Legnonotus* too). Secondary transverse rows are rare; among chondrosteans they may occur close to the dorsal and anal fins, as in *Bourbonella* ('écailles de transition'; Heyler 1969 : fig. 113) and *Paramblypterus* (Blot 1966 : fig. 17), or at the base of the axial lobe of the caudal fin (Hutchinson 1973 : 331). In the halecostome *Aphanepygus*, secondary scale-rows occur on the cheek and across the entire width of the trunk in the anterior region. In this form, the secondary scales are more numerous than those of the adjacent primary rows, from which they also differ in shape. Although this genus was placed in the Macrosemiidae by Bassani (1879), there is no sound evidence to support its retention within this family (Bartram 1977).

Areas of trunk devoid of scales occur in diverse fossil groups. Scales may be absent from the entire body with the exception of the axial lobe, as in the palaeoniscoids *Birgeria* and *Carboveles*, or from the posterior half of the trunk, as in the pycnodont *Macromesodon* and the 'semionotid' *Hemicalypterus* (Schaeffer 1967 : fig. 12). Apart from *Macrosemius* and *Legnonotus*, only '*Macrosemius*' *maeseni* (Saint-Seine in Saint-Seine & Casier 1962 : fig. 2) displays a scale-free area confined to a strip on either side of the dorsal fin. This fish probably belongs to the chondrostean genus *Tanaocrossus* Schaeffer (see p. 207). The regions on either side of the dorsal and anal fins are the last to form scales in ontogeny; among fish with rhomboid scales, scale-free areas in these locations have been found in juveniles of *Parasemionotus labordei*, *Pteronisculus cicatrosus* (Lehman 1952 : pl. 33a, c) and in the teleost *Wadeichthys oxyops* (Waldman 1971 : 30; pl. 16).

Thus the squamation of the macrosemiids offers no evidence of relationship with other neopterygian groups apart from *Uarbryichthys*.

The Macrosemiidae in relation to other Actinopterygians

Of the families of fossil actinopterygians recognized today, Thiollière's Macrosemiidae was among the earliest to be founded. In a summary of his conclusions following work upon the Jurassic fishes of Cerin (Thiollière 1858 : 782) he accepted Agassiz's family of the pycnodonts, while rejecting those of the sauroids and lepidoids. Thiollière recognized the need for a more 'natural' classification of the genera forming the last two groups, and noted that Pictet (1850) had begun well in erecting the family Leptolepidae. He proposed to establish a third family, the Macrosemiidae, 'qui réduira un peu le nombre de ces formes génèriques encore flottantes'.

He listed the genera forming the new family as *Macrosemius*, *Disticholepis* (= *Macrosemius*), *Histionotus*, *Notagogus*, *Propterus*, *Legnonotus* and *Rhynchoncodes* (= *Propterus*). These forms were considered by Thiollière to resemble one another in the structure of the skull, the form of the body, and in having an elongated dorsal fin. As is shown below, there is little doubt that the genera listed by Thiollière constitute a monophyletic group.

Woodward (1895) dealt with the phylogeny of the macrosemiids. He added the genus *Ophiopsis* to the family for the first time, and wrote of this form (**3** : 166): 'This is the least specialised genus ascribed to the Macrosemiidae and may be regarded as a link between this family and that of the Eugnathidae.' While *Ophiopsis* resembles the caturids, Woodward does not make clear his reasons for including this genus within the macrosemiids; they possess in common a long dorsal fin and a marked curvature of the mandible, and presumably he considered that these indicate relationship between the two.

Subsequent authors have all accepted in their classifications the link between *Ophiopsis* and the Macrosemiidae *sensu* Thiollière, and thus between the Macrosemiidae *sensu* Woodward and the caturids (Rayner 1941, Saint-Seine 1949, Berg 1955, Arambourg & Bertin 1958, Danil'chenko 1964, Lehman 1966, Romer 1966, Gardiner 1967, McAllister 1968).

Patterson (1973), in the knowledge that the present work was in progress, omitted the Macrosemiidae from his scheme of holostean and teleostean relationships. In his classification, Patterson has attempted to express the hierarchy of phylogenetic relationships within the non-chondrostean actinopterygians (Neopterygii). This has involved the definition of monophyletic groups in terms of specialized characters believed to have been commonly derived. If, as in the case of caturids and pholidophorids, no such specializations can be found, the paraphyletic nature of the group is admitted. The cladistic approach towards classification replaces the traditional typological identification of groups. The latter approach, based upon general resemblances shared by groups, is useless as a means of detecting relationships between them. When a typologically-recognized group, such as the Macrosemiidae *sensu* Thiollière, can be defined as a monophyletic group by the possession of shared specializations, this correspondence cannot be taken as a vindication of the typological approach. Rather, it must be treated as a special case, because the group is rich in derived characters.

Patterson's (1973) classification may be summarized as follows. He can find no evidence to suggest that *Lepisosteus* is descended from a group of fishes with a mobile maxilla or an interopercular; he places this genus in the division Ginglymodi, the sister-group of, and thus equal in rank to, the division Halecostomi, comprising the holosteans and teleosts. The halecostomes form two large sister-groups: the Halecomorphi (*Amia* and its fossil relatives), and the Teleostei (Recent teleosts and their fossil relatives). The relationships of the 'semionotids', probably a polyphyletic group, are unclear; they share none of the specializations of the halecomorphs or teleosts, and are considered to be basal halecostomes. Patterson stresses that the holosteans and teleosts need to be known in much greater detail before such a scheme can be accepted with confidence. Nevertheless his classification is used here as a working hypothesis, since it is sounder in method and wider in scope than any other.

The radical view of Jessen (1972), that the chondrosteans are more closely related to the teleosts than are the holosteans, is not accepted here. The implications that follow from it are most unlikely; either the chondrosteans retained mostly primitive actinopterygian characters (except in the pectoral girdle) and the holosteans and teleosts evolved in parallel to an improbable extent, or the many characters shared by holosteans and teleosts are primitive and those of the chondrosteans derived. These alternatives are equally unacceptable on present evidence.

There is no doubt that the macrosemiids are neopterygians. They display the following neopterygian specializations as identified by Patterson (1973).

1. Axial lobe of tail reduced.
2. Fin-rays equal in number to their supports in dorsal and anal fins.
3. Premaxilla immobile with a nasal process lining the nasal pit.
4. Vomer present.
5. Articular with a coronoid process.
6. Suspensorium upright and preopercular with a narrow dorsal arm.
7. Symplectic present.
8. Clavicles reduced.

Macrosemiids exhibit 21 specializations relative to the primitive neopterygian condition. The first two following are unique among actinopterygians and indicate that the Macrosemiidae *sensu* Thiollière constitute a monophyletic group; the genera in which each specialization is known to be present are given in parentheses. The genera *Ophiopsis*, *Songanella*, *Aphanepygus* and *Uarbryichthys*, which have been placed in the Macrosemiidae since Thiollière's publications, share neither of these specializations.

1. Nine infraorbitals, of which the first seven are scroll-like and the two behind the eye tubular. (*Macrosemius*, *Propterus*, *Histionotus*.) Although mormyriform teleosts have infraorbitals of similar shape, there are fewer than in the macrosemiids (Taverne 1971).

2. Interopercular small and remote from the mandible. (Known in all genera except *Legnonotus* and *Enchelyolepis*.) In all other groups the anterior end of the interopercular maintains a close proximity to the hind end of the lower jaw.

Macrosemiids share the following specializations with the Ginglymodi (*Lepisosteus*).

3. Absence of the opisthotic. (*Macrosemius*.) This is not unique; it is absent too in the halecostomes *Lepidotes*, *Amia* and the post-pholidophorid teleosts (Patterson 1975).

4. Extension of the exoccipital beyond the vagus canal. (*Macrosemius*.) This character also occurs in *Lepidotes* and post-pholidophorid teleosts (Patterson 1975).

5. Absence of the gular. This bone is also absent in *Acentrophorus*, *Lepidotes* and in all Recent teleosts except *Albula*, *Megalops* and *Elops*.

The macrosemiids possess none of the specializations of *Lepisosteus* identified by Patterson (1973 : 262) as unique (holospondylous, opisthocoelous centra; teeth with plicidentine; supraorbital canal running through premaxilla; a chain of toothed infraorbital bones). In contrast the macrosemiids share the following specializations with the Halecostomi, the sister-group of the Ginglymodi.

6. Mobile maxilla with a peg-like process anteriorly. (Known in all genera except *Legnonotus* and *Enchelyolepis*.)

7. Interopercular present.

8. Presence of uncinate processes on epibranchials. (*Macrosemius*.)

These specializations indicate that macrosemiids are halecostomes. Patterson (1973 : 262) identified several more halecostome specializations which are shared by teleosts (at the pholidophorid level) and halecomorphs. It is not known whether macrosemiids have a large posterior myodome or a large post-temporal fossa; both of these are present in *Lepidotes* and *Dapedium* too. Neither is it known whether the intercalar of Macrosemiidae has a membranous component. Two advanced halecostome characters are known to be missing in macrosemiids, however; these are the presence of a supramaxilla, and the loss of the quadratojugal as an independent element. Among halecostomes only *Acentrophorus* has no supramaxilla, and there is no evidence to suggest that its absence in macrosemiids is other than primitive. In all halecomorphs except *Furo longiserratus* (see p. 212) the quadratojugal is reduced to a small process on the quadrate or is absent altogether (*Amia*), and in teleosts the bone forms a splint-like outgrowth of the quadrate. The presence of an independent quadratojugal in a species of *Furo* suggests that it was independent too in the common ancestor of halecomorphs and teleosts, and that it became fused to the quadrate in parallel in these two groups. Thus the presence of an autogenous quadratojugal in macrosemiids (found also in *Lepisosteus*, *Lepidotes* and *Dapedium*; Patterson 1973) does not debar this group from membership of either the halecomorphs or teleosts. But the absence of a supramaxilla suggests that the macrosemiids belong to neither subdivision and are basal halecostomes. This may be tested by asking whether the macrosemiids possess the specializations which define the halecomorphs and teleosts each as monophyletic groups.

According to Patterson (1973 : 287) there is only one specialization unique to the Halecomorphi (Parasemionotidae, Caturidae and Amiidae), namely the articulation between the symplectic and the lower jaw. The available material reveals no such articulation in the macrosemiids. As Patterson (1973 : 248–250) points out, this character is not definitely an advanced one since the small bone in contact with the quadrate region of the palate and with the hind end of the mandible in palaeoniscids may be a symplectic, as identified by Nielsen (1942 : figs 35, 36, 70). If this character is invalid as a specialization then the parasemionotids cannot be included within the halecomorphs. However, the remaining halecomorphs (Amiidae and Caturidae) do share unique specializations. Thus in *Amia*, *Caturus heterurus*, *Heterolepidotus* and *Macrepistius* the dermosphenotic is incorporated into the skull roof and enwraps the front surface of the sphenotic. Although the dermosphenotic forms part of the skull roof in *Notagogus* it has no enwrapping flange, and in other macrosemiid genera this bone appears to have been hinged to the skull roof. Another important halecomorph specialization is the form of the intercalar. In *Amia* and in caturids where the braincase is known this bone forms membranous outgrowths which extend over the outside of the saccular chamber (Patterson 1973 : 280). Unfortunately this region of the braincase remains unknown in macrosemiids.

Thus there is no evidence at present which indicates relationship of the macrosemiids to the Halecomorphi. There is good evidence, however, that *Ophiopsis*, which does not belong in the Macrosemiidae, is closely related to the well-known caturid *Macrepistius* (Bartram 1975).

Patterson (1973) has marshalled an impressive set of unique specializations which define teleosts and their fossil relatives as a monophyletic group (Teleostei *s. str.*). These occur at the pachycormid level and involve the snout region, the quadrate and associated bones, and the caudal endoskeleton.

Primitively, teleosts have small, mobile premaxillae associated with bones Patterson has named lateral dermethmoids. As described in the preceding section, the primitive neopterygian premaxilla is immovably fixed to the braincase by a stout nasal process; this may encircle the olfactory nerve. In teleosts, in contrast, the premaxillae are small and mobile and the nasal processes are represented by separate lateral dermethmoid bones which in pholidophorids may also encircle the olfactory nerve. Primitively, as in *Pachycormus* and certain pholidophorids, these elements bear teeth. In pachycormids and living teleosts the lateral dermethmoids fuse with the rostral forming a rostro-dermethmoid; in higher teleosts this bone becomes incorporated into the mesethmoid. In the Macrosemiidae the premaxillae form nasal processes which are sutured with the braincase, and thus do not display the teleostean specialization.

In teleosts the quadratojugal forms a spine on the quadrate, the two receiving the symplectic in a groove along the inner surface. Although fusion occurs between quadratojugal and quadrate in some macrosemiids, in none is the quadratojugal as completely united with the quadrate as it is in Recent teleosts or even in pholidophorids. Although the symplectic of macrosemiids is not surely known, in *Macrosemius* at least no groove is formed for it on the inner surface of the quadrate.

The teleosts are unique in having uroneurals, neural arches which have elongated to stiffen the caudal fin. Patterson has found them in all groups usually related to the teleosts (at least those in which the caudal endoskeleton is known), and in the Pachycormidae. The caudal endoskeleton of macrosemiids is known only in two specimens of *Enchelyolepis*; these are very small and may be immature. However, they provide no evidence of uroneurals; the neural arches are small and scarcely ossified, in contrast with the stout, median, epurals.

Thus the Macrosemiidae show no evidence of relationship to either the teleosts or halecomorphs and so must be considered to be basal halecostomes.

The remaining specializations relative to the primitive neopterygian condition which the macrosemiids display are as follows.

9. Preopercular sensory canal exposed by large fenestrae at the base of the dorsal arm and along the entire length of the lower arm of the preopercular. The preopercular canal is similarly exposed in many teleosts (*Albula*, *Gymnarchus*, *Notopterus*, for example).
10. Supratemporals reduced and excluded from the midline; the medial part of the supratemporal commissure is borne by the parietals, which have probably fused with the medial supratemporals. (*Macrosemius*, *Propterus*, *Histionotus*.) This condition is found in many teleosts (McDowell 1973 : 12).
11. Frontals constricted in the preorbital region of the skull and housing the supraorbital canal in a gutter. (Known in all genera except *Enchelyolepis*.) This condition is very common in several groups of teleosts.
12. Nasals scroll-like. (*Macrosemius*, *Propterus*.) This condition is again found in many teleosts.
13. Suborbitals absent. Suborbitals have also been lost within the halecomorphs (*Amia*) and within the teleosts (all post-pholidophorid teleosts; Patterson 1973).
14. Hyomandibular bearing lateral flange. (*Macrosemius*, *Propterus*, *Histionotus*.) Such a flange is also present in *Perca* (Osse 1969).
15. Jaw articulation below the front of the orbit. (All macrosemiids.) This character appears in most neopterygians with short jaws (*Lepidotes*, *Pleuropholis*, *Megalops*, *Chanos*).
16. Lower margin of mandible concave in lateral view. (All macrosemiids.) A less marked curvature of the lower jaw is also found in *Ophiopsis*, the zeiform *Capros* and in mormyrids.
17. Mandibular sensory canal housed in wide gutter in the dentary and angular. (All macrosemiids.) Mormyrids and many other teleosts display this feature.
18. Upper branchiostegals acinaciform. (*Macrosemius*, *Propterus*.) Acinaciform branchiostegals are widespread among acanthopterygian teleosts (McAllister 1968 : pls 11–19).
19. Proximal ceratohyal short and deep posteriorly. (*Macrosemius*, *Propterus*, *Notagogus*.) The ceratohyal is similar in mormyrids and many acanthopterygians (McAllister 1968 : pls 11–19).
20. Serrated appendage present. (*Propterus*.) Such an appendage is also known in *Amia* and *Caturus*; it is absent in teleosts.
21. Dorsal fin very long. This character is found in many groups (Amiidae, 'Semionotidae' and many teleost families).

In summary, the Macrosemiidae are a group of neopterygians which display 21 specializations, listed above, relative to the primitive neopterygian condition. The first two of these are unique and indicate that the macrosemiids form a monophyletic group. *Ophiopsis*, *Songanella*, *Aphanepygus* and *Uarbryichthys* do not have them, and are thus not included within the family. Owing to scarcity of specimens and mode of preservation, these two specializations are not known to be present in *Legnonotus* and *Enchelyolepis* either. Thus, strictly, they too should be excluded from the macrosemiids. *Legnonotus* shares with *Macrosemius*, however, a unique specialization, the absence of scales from the region on either side of the dorsal fin. *Legnonotus* is retained in the macrosemiids for this reason. Far less confidence can be had in the retention of *Enchelyolepis* within the macrosemiids, although having re-examined the specimens I feel that Woodward was right in placing them within that family. *Enchelyolepis* is retained here in the Macrosemiidae until more information is available.

In spite of this study, knowledge of the structure of the Macrosemiidae remains far from complete. This lessens the chances of accuracy in placing the group in a phylogenetic classification. Much more needs to be known, for example, about the braincase and the caudal fin, and hopefully, despite the scarcity of suitable material, these structures will eventually be described.

What is known about the macrosemiids, however, indicates that this family arose before the divergence of the halecomorph and teleost halecostomes. Since they show no evidence of relationship to any other holostean group, they have been classified here as Halecostomi, subdivision *incertae sedis*. The snout and jaw articulation of macrosemiids both display the primitive neopterygian condition, and if *Enchelyolepis* is indeed a macrosemiid, so too does the caudal endoskeleton. It is perhaps surprising then to find that so many macrosemiid specializations are also found in teleosts. But some of these (11–13, 17, 19 above) are evidently due to a tendency within the family to lose laminar bone, while others (10, 14) are due to the relative shortness of the postorbital region of the skull, or (15, 20) to the shortness of the jaws.

Relationships within the Macrosemiidae

The macrosemiids present a variety of form unusual among holostean groups. By analysing these variable characters, the interrelationships of the genera within the family may be suggested. The following specializations occur within the Macrosemiidae:

1. Dorsal fin divided (*Notagogus*, *Histionotus*, *Propterus*). Apart from the macrosemiids and polypterids, divided dorsal fins are unknown among non-teleost actinopterygians. A long, undivided dorsal fin is undoubtedly the primitive macrosemiid condition; such a fin occurs in *Uarbryichthys*.
2. Scales absent on either side of the dorsal fin (*Macrosemius*, *Legnonotus*).
3. Ganoine on scales reduced (*Macrosemius*, *Propterus*).
4. Trunk shallow (*Macrosemius*, *Legnonotus*). There are several indications that macrosemiids were primitively deep-bodied, as are *Uarbryichthys*, *Histionotus* and *Propterus*. Both Gregory (1933 : 131) and Saint-Seine (1949 : 196) mention that the macrosemiid skull is reminiscent of those of deep-bodied fish. The origin of the family from fishes with deep bodies may also account for the presence of the elongated dorsal fin, since the two features are often associated as Gregory also points out. This association occurs in *Uarbryichthys*.
5. Caudal fin weakly forked or rounded, with a reduced number of rays (*Macrosemius*, *Legnonotus*, *Notagogus*). The tail of *Histionotus* is probably the most primitive; it is deeply forked, with the highest number of rays.
6. Surface of parietals forming stout ridges (*Histionotus*, *Propterus*). This unusual feature is unknown among other holosteans. The smooth skull roof of *Notagogus* and *Macrosemius* is undoubtedly primitive.
7. Quadratojugal notched close to distal end (*Propterus*, *Histionotus*).
8. Maxillary teeth reduced (*Macrosemius*, *Propterus*) or absent (*Histionotus*). The full row of teeth displayed by *Notagogus* and *Legnonotus* is presumably primitive for the family.
9. Reduction or loss of fringing fulcra on dorsal fin (*Macrosemius*, *Propterus elongatus*, *P. microstomus*, *Notagogus*), anal fin (*Macrosemius*, *Notagogus*) and paired fins (*Propterus elongatus*, *Macrosemius*, *Notagogus*).
10. Sensory canals in the posterior part of the skull roof large and exposed by large fenestrae (*Macrosemius*, *Histionotus*, *Propterus*). In *Notagogus* these canals are narrow and completely

enclosed; this is probably the primitive macrosemiid condition, since it is found also in *Uarbryichthys*.

11. Dermosphenotic not incorporated into skull roof and not enclosing the junction between infra- and supraorbital canals (*Macrosemius*, *Histionotus*, *Propterus*).

12. Anterior dorsal fin emarginate (*Histionotus*, *P. microstomus*).

Characters 6 and 7 unite *Propterus* and *Histionotus*, and characters 2 and 4 unite *Macrosemius* and *Legnonotus* as monophyletic groups, with little doubt. If this is correct, then the relationship between *Notagogus* and these two macrosemiid subgroups is not easy to determine. Although this genus shares specialization 5 with *Macrosemius – Legnonotus*, it also shares specialization 1 with *Histionotus – Propterus*. But if *Notagogus* is placed in either group it demands that specializations 10 and 11 arose within the family twice, which seems unlikely. It is more reasonable then to place *Notagogus* as the sister-group of the other four genera, and assume that the divided dorsal fin and reduced caudal fin were acquired in parallel by this genus. The genus *Enchelyolepis* is too ill-known at present to be fitted into this scheme of relationships.

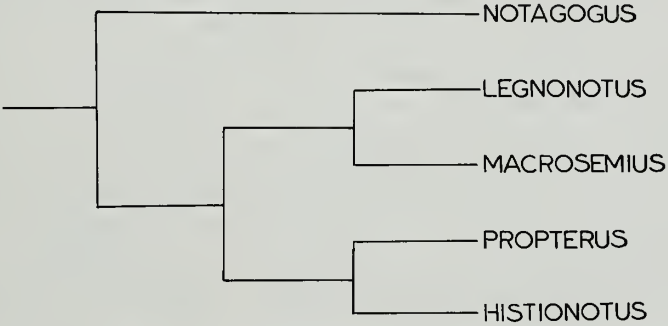

Fig. 53 Suggested interrelationships within the Macrosemiidae.

In summary, the variable characters of the macrosemiids were primitively in the following states: dorsal fin undivided; squamation entire; ganoine covering on scales entire; trunk deep; caudal fin deeply forked with at least 16 rays; surface of parietals smooth; quadratojugal without notches; oral margin of maxilla bearing full row of teeth; fringing fulcra on all fins; sensory canals on skull roof fully enclosed by bone; dermosphenotic incorporated into skull roof. All these are found primitively in Neopterygii and, with the possible exception of the maxillary teeth, in *Uarbryichthys*, the plesiomorph sister-group of the macrosemiids. *Notagogus* acquired a divided dorsal fin, a less strongly forked caudal fin, and a depressed trunk. This genus forms the sister-group of all the other macrosemiids, whose skull roof sensory canals became exposed by large fenestrae, and whose dermosphenotics became reduced. *Macrosemius* and *Legnonotus* are most closely related to each other, as indicated by the loss of the dorsal squamation. In parallel with *Notagogus*, however, these two genera acquired a depressed trunk and a reduced caudal fin; they retained the continuous dorsal fin. *Histionotus* and *Propterus* are united by the notched quadratojugal, and by the ridged parietals; they acquired divided dorsal fins in parallel with *Notagogus*, and a reduced maxillary dentition in parallel with *Macrosemius*.

Ecological note

The macrosemiids are represented in the Triassic by *Legnonotus* only, and none occur in the Lower Jurassic. Thus no members of this family formed part of the Triassic marine faunas of Italy, or of the great Lias faunas preserved at Lyme Regis and Holzmaden. Most species and specimens of macrosemiids have been recovered from Upper Jurassic and Lower Cretaceous deposits associated with reef-building organisms. Thus *Macrosemius*, *Propterus*, *Notagogus* and *Histionotus* occur in the Lithographic Limestones of Bavaria and Cerin, and *Propterus* and *Notagogus* occur too in those of Lerida in Spain. These deposits were laid down offshore under calm conditions, protected from the open sea by a barrier reef (Saint-Seine 1949, Barthel 1970). It seems that the Macrosemiidae were adapted to, and perhaps largely confined to, the reef environment; it would be surprising if none were found at the recently-discovered Upper Jurassic fossiliferous locality at Canjuers (Var, France).

According to Barthel, the floor of the Bavarian lagoon was raised into ridges formed by sponge and algal reefs. Coral reefs grew on some of these, forming the barrier which defined the lagoon. Fine calcareous particles were brought in from the open sea, and settled on its floor between the ridges. The reefs supported a large population of benthonic crustaceans; although preserved in the calcareous mud, few have left their tracks there, and Barthel takes this as evidence that conditions on the floor of the lagoon were lethal.

Two broad categories of food must have been available to the fishes in this environment. The first comprised fast-moving prey, such as cephalopod molluscs and fish. Such prey was available to large fish with highly-forked tails, small fins and a large gape armed with sharp teeth, for example *Caturus*, *Pholidophorus*, *Aspidorhynchus* and *Thrissops*. The second category includes stationary food (algae, corals, detritus) and comparatively slow-moving animals (benthonic molluscs and crustaceans). Such food would have been taken by fishes with small mouths, moving relatively slowly and relying on the reefs for shelter from predators.

It seems that the macrosemiids belong with the latter group. Their small gape, reduction of the maxillary teeth and stoutness of the remaining dentition indicate that these fishes took algae or small armoured prey. The large surface area of the fins of macrosemiids suggests that they moved slowly but with great manœuvrability through the reefs. The stout sharp basal fulcra on the tails of *Macrosemius* and *Propterus* would have deterred attack from the rear.

At least two examples are known of macrosemiid-as-prey. A specimen of *Ionoscopus desori* (LM 15.313) has a *Notagogus* in its abdomen, and a specimen of *Belonostomus tenuirostris* (LM 15.509) has another individual of the same genus in its jaws (Saint-Seine 1949 : 182; pl. 24, fig. C).

References

Agassiz, L. 1833–44. *Recherches sur les poissons fossiles.* **1–5**, 1420 pp., 396 pls, with supplement. Neuchâtel. (For dates of publication see Woodward & Sherborn 1890.)

—— 1834. Abgerissene Bemerkungen über fossile Fische. *Neues Jb. Miner. Geogn. Geol. Petrefakt.*, Stuttgart, **1834** : 377–390.

Allis, E. P. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva. J. Morph.*, Boston, **12** : 487–808, 38 pls.

—— 1903. The skull, and the cranial and first spinal nerves in *Scomber scomber. J. Morph.*, Philadelphia, **18** : 45–328, 12 pls.

Arambourg, C. & Bertin, L. 1958. Super-ordre des Holostei. *In* Grassé, P. P. (ed.), *Traité de Zoologie* **13** (3) : 2174–2194, figs 1536–1556. Paris.

Baglioni, S. 1907. Der Atmungsmechanismus der Fische. *Z. allg. Physiol.*, Jena, **7** : 177–182.

Barthel, K. W. 1970. On the deposition of the Solnhofen lithographic limestone (Lower Tithonian, Bavaria, Germany). *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **135** : 1–18, 4 pls, 2 figs.

Bartram, A. W. H. 1975. The holostean fish genus *Ophiopsis* Agassiz. *Zool. J. Linn. Soc.*, London, **56** : 183–205, 8 figs.

—— 1977. A problematical Upper Cretaceous holostean fish genus *Aphanepygus. J. nat. Hist.*, London, **11** (4) : 361–370, 5 figs.

Bassani, F. 1879. Vorläufige Mittheilungen über die Fischfauna der Insel Lesina. *Verh. geol. Reichsanst.* (*StAnst-Landesanst.*), *Wien*, **1879** : 162–170.

—— 1882. Descrizione dei pesci fossili di Lesina accompagnata da appunti su alcune altre ittiofaune cretacee (Pietraroia, Voirons, Comen, Grodischtz, Crespano, Tolfa, Hakel, Sahel-Alma e Vestfalia). *Denkschr. Akad. Wiss. Wien*, **45** : 195–288, 16 pls.

—— & d'Erasmo, G. 1912. La Ittiofauna del calcare cretacico di Capo d'Orlando presso Castellamare (Napoli). *Memorie Mat. Fis. Soc. ital. Sci.*, Rome, **17** : 185–243, 6 pls.

Bataller, G. 1956. La paleontológia y Luis Mariono Vidal. *Boln Inst. geol. min. Esp.*, Madrid, **67** : 1–50, 14 pls.

Berg, L. S. 1955. [Classification of fishes and fish-like vertebrates, both recent and fossil.] 2nd ed. *Trudӯ zool. Inst. Leningr.* **20** : 1–286, 263 figs. (In Russian.)

Bjerring, H. 1972. The rhinal bone and its evolutionary significance. *Zoologica Scr.*, Stockholm, **1** : 193–201, 6 figs.

Blot, J. 1966. *Étude des Palaeonisciformes du Bassin de Commentry.* 99 pp., 18 pls, 29 figs. Paris, Centre Nationale de la Recherche Scientifique.

Brenner, P., Geldmacher, W. & Schroeder, R. 1974. Ostrakoden und Alter der Plattenkalke von Rubies (Sierra de Monsech, Prov. Lerida, NE-Spanien). *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **1974** : 513–524, 1 fig.

Brough, J. 1939. *The Triassic fishes of Besano, Lombardy.* ix + 117 pp., 7 pls. London, Brit. Mus. (Nat. Hist.).

Costa, O. G. 1850–64. Paleontologia del Regno di Napoli . . . (&c.), [1]. *Atti Accad. pontan.*, Naples, **5** : 233–433 (1850). 2. *loc. cit.* **7** : 1–378, 28 pls (1853). 3. *loc. cit.* **8** : 1–196, 16 pls (1864).

Danil'chenko, P. G. 1964. Superorder Holostei. *In* Obruchev, D. V. (ed.), *Osnovy Paleontologii* **11** : 378–395, figs 74–100. Moskow, Akad. Nauk SSSR. (In Russian.)

Eastman, C. R. 1914. Catalog of the fossil fishes in the Carnegie Museum. 3, Catalog of fossil fishes from the lithographic stone of Cerin, France. *Mem. Carneg. Mus.*, Pittsburgh, **6** : 349–388, 9 pls. 4, Descriptive catalog of fossil fishes from the lithographic stone of Solenhofen, Bavaria. *loc. cit.* **6** : 389–423, 17 pls. (1914a).

—— 1917. Fossil fishes in the collection of the United States National Museum. *Proc. U.S. natn. Mus.*, Washington, **52** : 235–304, pls 1–23.

Edgeworth, F. H. 1935. *The cranial muscles of vertebrates.* ix + 493 pp., 841 figs. Cambridge.

Egerton, P. de M. G. 1854. On some new genera and species of fossil fishes. *Ann. Mag. nat. Hist.*, London, (2) **13** : 433–436.

—— 1855. Figures and descriptions of British Organic Remains, dec. **9** : 1–34, 10 pls. *Mem. geol. Surv. U.K.*, London.

Erasmo, G. d'. 1914. La fauna e l'età dei calcari a ittioliti di Pietraroia (Prov. di Benevento). *Palaeontogr. ital.*, Pisa, **20** : 29–86, pls 4–10.

Gardiner, B. G. 1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **4** : 239–384, pls 36–43, 81 figs.

—— 1967. The significance of the preoperculum in actinopterygian evolution. *J. Linn. Soc.* (Zool.), London, **47** : 197–209, 8 figs.

Gill, E. L. 1923. The Permian fishes of the genus *Acentrophorus*. *Proc. zool. Soc. Lond.* **1923** : 19–40, 16 figs.

Goodrich, E. S. 1930. *Studies on the structure and development of vertebrates.* xxx + 837 pp., 754 figs. London.

Gorjanovic-Kramberger, K. 1905. Die Obertriadische Fischfauna von Hallein in Salzburg. *Beitr. Paläont. Geol. Öst.-Ung.*, Vienna & Leipzig, **18** : 193–224, pls 17–21, 20 figs.

Gosline, W. A. 1965. Teleostean Phylogeny. *Copeia*, Ann Arbor, **1965** : 186–194, 1 fig.

—— 1967. Reduction in branchiostegal ray number. *Copeia*, Ann Arbor, **1967** : 237–239, 1 fig.

—— 1969. The morphology and systematic position of the Alepocephaloid fishes. *Bull. Br. Mus. nat. Hist.* (Zool.), London, **18** : 183–218, 14 figs.

Gregory, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. *Trans. Am. phil. Soc.*, Philadelphia, **23** : i–vii, 75–481, 302 figs.

Griffith, J. & Patterson, C. 1963. The structure and relationships of the Jurassic fish *Ichthyokentema purbeckensis*. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **8** : 1–43, 4 pls, 14 figs.

Harris, J. E. 1937. The mechanical significance of the position and movements of the paired fins in the Teleostei. *Pap. Tortugas Lab.*, Washington, **31** : 171–189, 8 figs.

Heyler, D. 1969. *Vertébrés de l'Autunien de France.* 259 pp., 52 pls, 166 figs. Paris, Centre Nationale de la Recherche Scientifique.

Holmgren, N. & Stensiö, E. A. 1936. Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. *In* Bolk, L. *et al.* (eds), *Handbuch der vergleichenden Anatomie der Wirbeltiere* **4** : 233–500, figs 203–373. Berlin & Vienna.

Hutchinson, P. 1973. A revision of the Redfieldiiform and Perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bull. Br. Mus. nat. Hist.* (Geol.), London, **22** : 233–354, 54 figs.

Jarvik, E. 1944. On the exoskeletal shoulder girdle of teleostomian fishes, with special reference to *Eusthenopteron foordi* Whiteaves. *K. svenska VetenskAkad. Handl.*, Stockholm, (3) **21**, 7 : 1–32, 9 figs.

—— 1967. The homologies of frontal and parietal bones in fishes and tetrapods. *Colloques int. Cent. natn. Rech. scient.*, Paris, **163** : 181–213, 4 pls.

Jessen, H. 1968. The gular plates and branchiostegal rays in *Amia*, *Elops* and *Polypterus*. *In* Ørvig, T. (ed.), *Current Problems of Lower Vertebrate Phylogeny* : 429–438, 3 figs. Stockholm (Nobel Symposium 4).

—— 1972. Schultergürtel und Pectoralflosse bei Actinopterygiern. *Fossils Strata*, Oslo, **1** : 1–101, 25 pls, 11 figs.

Kapoor, A. S. 1970. Development of dermal bones related to sensory canals of the head in the fishes *Ophicephalus punctatus* Bloch (Ophicephalidae) and *Wallago attu* Bl. & Schn. (Siluridae). *Zool. J. Linn. Soc.*, London, **49** : 69–97, 4 pls, 47 figs.

Kerr, T. 1952. The scales of primitive living actinopterygians. *Proc. zool. Soc. Lond.* **122** : 55–78, 2 pls, 5 figs.

Lehman, J.-P. 1949. Étude d'un *Pachycormus* du Lias de Normandie. *K. svenska VetenskAkad. Handl.*, Stockholm, (4) **1**, 2 : 1–44, pls 1–9.

—— 1952. Étude complémentaire des Poissons de l'Éotrias de Madagascar. *K. svenska VetenskAkad. Handl.*, Stockholm, (4) **2**, 6 : 1–201, 48 pls.

—— 1966. Actinopterygii. *In* Piveteau, J. (ed.), *Traité de Paléontologie* **4** (3) : 1–242, figs 1–211. Paris.

Liem, K. F. 1967. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other Recent teleosts. *J. Morph.*, Philadelphia, **121** : 103–104 23 figs.

—— **& Woods, L. P.** 1973. A probable homologue of the clavicle in the holostean fish *Amia calva*. *Proc. zool. Soc. Lond.* **170** : 521–531, 4 pls.

McAllister, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *Bull. natn. Mus. Can.*, Ottawa, **221** : xiv + 239 pp., 21 pls.

McDowell, S. B. 1973. Order Heteromi (Notacanthiformes). *In* Fishes of the Western North Atlantic. *Mem. Sears Fdn mar. Res.*, New Haven, **1** (6) : 1–31, 5 figs.

Mansell-Pleydell, J. C. 1889. On a new specimen of *Histionotus angularis* Egerton. *Geol. Mag.*, London, (3) **6** : 241–242, 1 pl.

Marshall, N. B. 1971. *Explorations in the life of fishes.* 204 pp., 54 figs. Cambridge, Mass.

Millard, N. A. H. 1966. Contributions to the functional morphology of fishes, 1. Introduction. *Zoologica afr.*, Cape Town, **2** : 31–43.

Nelson, G. J. 1973. Relationships of clupeomorphs, with remarks on the structure of the lower jaw in fishes. *In* Greenwood, P. H., Miles, R. S. & Patterson, C. (eds), *Interrelationships of fishes. Zool. J. Linn. Soc.*, London, **53**, suppl. 1 : 333–349, 8 figs.

Nielsen, E. 1942. Studies on Triassic fishes from East Greenland, 1. *Glaucolepis* and *Boreosomus*. *Meddr Grønland*, Copenhagen, **138** : 1–403, 30 pls, 78 figs.

—— 1949. Studies on Triassic fishes from East Greenland, 2. *Australosomus* and *Birgeria*. *Meddr Grønland*, Copenhagen, **146** : 1–309, 20 pls, 82 figs.

—— 1955. Notes on Triassic Fishes from Madagascar, 1. *Errolichthys mirabilis* Lehman. *Meddr dansk geol. Foren.*, Copenhagen, **12** : 563–578, 11 figs.

Nybelin, O. 1960. A gular plate in *Albula vulpes* (L.). *Nature, Lond.* **188** (4744) : 78, 1 fig.

Osse, J. W. M. 1969. Functional morphology of the head of the Perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.*, Leiden, **19** : 289–392, 24 figs.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes with special reference to those of the English Chalk. *Phil. Trans. R. Soc.*, London, B **247** : 213–482, pls 2–5, 103 figs.

—— 1968. The caudal skeleton in Lower Liassic pholidophorid fishes. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **16** : 201–239, 5 pls, 12 figs.

—— 1973. Interrelationships of holosteans. *In* Greenwood, P. H., Miles, R. S. & Patterson, C. (eds), *Interrelationships of fishes. Zool. J. Linn. Soc.*, London, **53**, suppl. 1 : 233–305, 27 figs.

—— 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Phil. Trans. R. Soc.*, London, B **269** : 275–579, 13 pls, 151 figs.

Pehrson, T. 1940. The development of dermal bones in the skull of *Amia calva*. *Acta zool. Stockh.* **21** : 1–50, 50 figs.

Pictet, F. J. 1850. *Déscription de quelques poissons fossiles du Mont Liban.* 59 pp., 10 pls. Geneva.

Poplin, C. 1974. *Étude de quelques paléoniscidés pennsylvaniens du Kansas.* 148 pp., 40 pls, 48 figs. Paris, Centre Nationale de la Recherche Scientifique.

Rayner, D. H. 1941. The structure and evolution of the holostean fishes. *Biol. Rev.*, Cambridge, **16** : 218–237, 12 figs.

—— 1948. The structure of certain Jurassic holostean fishes with special reference to their neurocrania. *Phil. Trans. R. Soc.*, London, B **233** : 287–345, pls 19–22, 34 figs.

Romer, A. S. 1966. *Vertebrate Paleontology*, 3rd ed. ix + 468 pp., 443 figs. Chicago.

Saint-Seine, P. de 1949. Les poissons des calcaires lithographiques de Cerin (Ain). *Nouv. Archs Mus. Hist. nat. Lyon*, **2** : vii + 357 pp., 26 pls.

—— 1955. Poissons fossiles de l'étage de Stanleyville (Congo Belge), 1. La faune des argilites et schistes bitumineux. *Annls Mus. r. Congo Belge*, Tervuren, sér. géol. 8°, **14**. xx+126 pp., 13 pls, 85 figs.

—— & **Casier, E.** 1962. Poissons fossiles des couches de Stanleyville (Congo), 2. La faune marine des calcaires de Songa. *Annls Mus. r. Afr. cent.*, Tervuren, sér. géol. 8°, **44**. xi+52 pp., 9 pls, 17 figs.

Sauvage, H.-E. 1883. Notes sur les poissons fossiles. *Bull. Soc. géol. Fr.*, Paris, (3) **6** : 475–503, pls 10–13.

—— 1893. Note sur quelques poissons du calcaire bitumineux d'Orbagnoux (Ain). *Bull. Soc. Hist. nat. Autun* **6** : 427–443, pls 8, 9.

—— 1903. Notica sobre los peces de la caliza litográfica de la provincia de Lérida (Cataluña). *Mems R. Acad. Cienc. Artes Barcelona* (3) **4**, 35 : 1–32, 5 pls.

Schaeffer, B. 1960. The Cretaceous Holostean fish *Macrepistius*. *Am. Mus. Novit.*, New York, **2011**. 18 pp., 9 figs.

—— 1967. Late Triassic fishes from the western United States. *Bull. Am. Mus. nat. Hist.*, New York, **135** : 285–342, 22 pls.

Schultze, H. P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **126** : 232–314, pls 49–53.

Stensiö, E. A. 1932. Triassic Fishes from East Greenland collected by the Danish expeditions in 1929–31. *Meddr Grønland*, Copenhagen, **83** (3) : 1–305, 39 pls, 94 figs.

Taverne, L. 1971. Ostéologie des genres *Marcusenius* Gill, *Hippopotamyrus* Pappenheim, *Cyphomyrus* Myers, *Pollimyrus* Taverne et *Brienomyrus* Taverne (Pisces Mormyriformes). *Annls Mus. r. Afr. cent.*, Tervuren, sér. zool. 8°, **188** : x+144 pp., 3 pls, 80 figs.

Thiollière, V. 1850. Seconde notice sur le gisement et les fossiles d'origine organique des calcaires lithographiques, dans le Jura du Département de l'Ain . . . (&c.). *Annls Sci. Phys. nat. Lyon* (2) **3** : 111–184, pls 3, 4.

—— 1854–73. *Descriptions des poissons fossiles provenant des gisements coralliens du Jura dans le Bugey.* **1**, 27 pp., 10 pls (1854). **2**, 70 pp., 16 pls (1873). Lyons.

—— 1858. Note sur les poissons fossiles du Bugey, et sur l'application de la méthode de Cuvier à leur classement. *Bull. Soc. géol. Fr.*, Paris, (2) **15** : 782–793.

Toombs, H. A. & Rixon, A. E. 1959. The use of acids in the preparation of vertebrate fossils. *Curator*, New York, **2** : 304–312, 4 figs.

Traquair, R. H. 1911. Les poissons wealdiens de Bernissart. *Mém. Mus. r. Hist. nat. Belg.*, Brussels, **5** : iv+65 pp., 12 pls.

Vianna, E. A. 1949. Un peixe do Lusitaniano do Cabo Mondego. *Comunçoes Comm. Trab. Serv. geol. Port.*, Lisbon, **30** : 13–21, 1 pl.

Vetter, B. 1881. Die Fische aus den lithographischen Schiefer im Dresdener Museum. *Mitt. K. miner-geol. prähist. Mus. Dresden*, Cassel, **4** : 1–118, 3 pls.

Vrba, E. S. 1968. Contributions to the functional morphology of fishes, 5. The feeding mechanism of *Elops saurus* Linnaeus. *Zoologica afr.*, Cape Town, **3** : 211–236, 9 figs.

Wade, R. T. 1941. The Jurassic fishes of New South Wales. *J. Proc. R. Soc. N.S.W.*, Sydney, **75** : 71–84, 2 pls.

—— 1953. Jurassic fishes of New South Wales (Macrosemiidae) with a note on the Triassic genus *Promecosomina*. *J. Proc. R. Soc. N.S.W.*, Sydney, **87** : 63–72, pls 8–9.

Wagner, J. A. 1851. Beiträge zur Kenntnis der in den Lithographischen Schiefern abgelargerten urweltlichen Fische. *Abh. bayer. Akad. Wiss.*, Munich, **6**. 80 pp., 4 pls.

—— 1860. Vergleichung der urweltischen Fauna des lithographischen Schiefers von Cirin . . . (&c.). *Gel. Anz. Akad. Wiss. München*, **50** (48–51) : 390–412.

—— 1863. Monographie der fossilien Fische aus den Lithographischen Schiefern Bayerns. *Abh. bayer. Akad. Wiss.*, Munich, **9** (3) : 613–748, pls 2–7.

Waldman, M. 1971. Fish from the freshwater Lower Cretaceous of Victoria, Australia, with comments on the palaeo-environment. *Spec. Pap. Palaeont.*, London, **9**. 124 pp., 18 pls, 37 figs.

Watson, D. M. S. 1925. The structure of certain palaeoniscids and the relationships of that group with other bony fish. *Proc. zool. Soc. Lond.* **1925** : 815–870, 2 pls, 30 figs.

Wenz, S. 1964. Étude d'un nouveau *Notagogus* de la province de Lerida (Espagne). *Bull. Soc. géol. Fr.*, Paris, (7) **6** : 269–272, pl. 12b, 1 fig.

—— 1968. *Compléments à l'étude des poissons actinoptèrygiens du Jurassique français.* 276 pp., 48 pls, 110 figs. Paris, Centre Nationale de la Recherche Scientifique.

Westoll, T. S. 1944. The Haplolepidae, a new family of Late Carboniferous bony fishes. A study in taxonomy and evolution. *Bull. Am. Mus. nat. Hist.*, New York, **83** : 1–122, pls 1–10.

Wilder, B. 1876. On the serrated appendages in the throat of *Amia*. *Proc. Am. Ass. Advmt Sci.*, New York, **25** : 259–263, 1 fig.

Woodward, A. S. 1895. *Catalogue of the fossil fishes in the British Museum* (*Natural History*), **3**. xlii + 544 pp., 18 pls. London, Brit. Mus. (Nat. Hist.).

—— 1895a. A contribution to knowledge of the fossil fish fauna of the English Purbeck Beds. *Geol. Mag.*, London, (4) **2** : 145–152, 1 pl.

—— 1918. The fossil fishes of the English Wealden and Purbeck formations, **2** : 49–104, pls 11–20, figs 20–34. *Palaeontogr. Soc.* (*Monogr.*), London.

—— **& Sherborn, C. D.** 1890. *A catalogue of British fossil vertebrates.* xxxv + 396 pp. London.

Wright, R. R. 1884. On the function of the serrated appendages of the throat of *Amia*. *Science*, *N.Y.* **4** : 511.

Zittel, K. A. 1887–8. *Handbuch der Palaeontologie. I Abteilung, Palaeozoologie.* **3** (1–2) : 1–337, 323 figs. Munich & Leipzig.

Explanation of abbreviations used in text-figures

Adp	anterior dermopalatine
Ang	angular
Ant	antorbital
ap	ascending process of parasphenoid
apl	anterior pit-line on parietal
Art	articular
axs	scales of axial lobe of caudal fin
bf	basal fulcrum
Boc	basioccipital
bpr	basipterygoid process of parasphenoid
Brr	branchiostegal ray
c	centrum
cbr	ceratobranchial
cc	position of crus communis of membranous labyrinth
Cl	cleithrum
Cor	coronoid
D	dentary
d	denticle
Dch	distal ceratohyal
Dpt	dermopterotic
dr	ray emanating from axial lobe of caudal fin
Dsp	dermosphenotic
E	ethmoid ossification
ebr	epibranchial
ec	ethmoidal commissural sensory canal
Ecp	ectopterygoid
Enp	endopterygoid
ep	epural
Epo	epioccipital
epsa	foramen for efferent pseudobranchial artery
Exo	exoccipital
F	frontal
fapf	foramen for anterior palatine ramus of facial nerve
ff	fringing fulcrum
fib	facet on epibranchial for articulation of pharyngobranchial
fm	foramen magnum
gac	groove on prearticular receiving process of coronoid
glf	glossopharyngeal foramen
gs	glenoid articulatory surface of mesocoracoid arch
h	hypural
Hb	hypobranchial
Hh	hypohyal
Hm	hyomandibular
hsc	horizontal semicircular canal
Ih	interhyal
Io	infraorbital
ioc	infraorbital sensory canal
Iop	interopercular
Las	lateral anal scale
lcc	lateral cranial canal
lf	lateral flange of hyomandibular
lp	lateral process of fin-ray
mc	mandibular sensory canal
Mco	mesocoracoid arch
mefc	foramen for external mandibular ramus of facial nerve
mll	main lateral line
mp	medial process of maxilla
mpl	middle pit-line on parietal
Mpt	metapterygoid
mr	middle segment of dorsal fin radial
Mx	maxilla
N	nasal
np	nasal process of premaxilla
Op	opercular
Ors	orbitosphenoid

P	parietal
pall	pit of accessory lateral line
Pans	postanal scale
Pas	parasphenoid
Pch	proximal ceratohyal
Pdp	posterior dermopalatine
Pmx	premaxilla
Pop	preopercular
Pos	preanal scale
pp	pedicel on parasphenoid
pr	proximal fin radial
Pra	prearticular
Pro	prootic
Prop	propterygium of pectoral fin
psc	posterior semicircular canal
Pte	pterosphenoid
Pto	pterotic
ptsr	primary transverse scale-row
Ptt	post-temporal
pu	preural centrum
puhs	preural haemal spine
Q	quadrate
Qj	quadratojugal
R	rostral
r	fin-ray
Rar	retroarticular
S	symplectic
sac	position of sacculus
Sang	surangular
Scl	supracleithrum
Ser	serrated appendage
So	supraorbital(s)
soc	supraorbital sensory canal
Sop	subopercular
Sph	sphenotic
spl	splint(s) preceding leading fin-ray
stc	supratemporal commissural sensory canal
stsr	secondary transverse scale-row
Stt	supratemporal
tp	transverse process of centrum
ud	urodermal
up	uncinate process on epibranchial
V	vomer
vp	ventral process of fin-ray
IX	glossopharyngeal foramen
X	vagus foramen

Index

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.